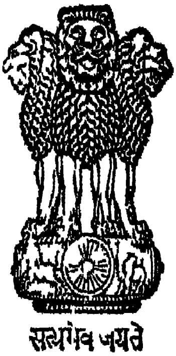

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A BIOGEOGRAPHICAL STUDY OF THE ORDINOIDES ARTENKREIS OF GARTER SNAKES (GENUS THAMNOPHIS)

BY

HENRY S. FITCH

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOÖLOGY

EDITORS (Berkeley): J. F. DANIEL, HAROLD KIRBY, S. F. LIGHT, A. H. MILLER

Volume 44, No. 1, pp. 1–150, plates 1–7,
21 figures in text
Submitted by editors January 17, 1938
Issued October 31, 1940
Price, $1.50

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY, CALIFORNIA

CAMBRIDGE UNIVERSITY PRESS
LONDON, ENGLAND

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(Contribution from the University of California Museum of Vertebrate Zoölogy)

INTRODUCTION

FIELD ACQUAINTANCE with three supposed subspecies of the garter snake, *Thamnophis ordinoides*, which occurred in the same general region in southwestern Oregon, first aroused my interest in this group of snakes. These so-called subspecies seemed to be separated only by habitat differences. This unusual circumstance, combined with abundance of individual garter snakes, wide geographic range under diverse environmental conditions, and great variability, recommended the western forms of *Thamnophis* as a group unusually favorable for comparative ecological study. The problem in systematy was therefore undertaken with the idea of employing ecologic as well as morphologic characters in determining relationships.

Although my conclusions regarding the relationships of the different races are often at variance with those of Van Denburgh and Slevin (1918), their work has been used as a basis for the present study, and special attention has been directed toward problems raised, but not satisfactorily solved, by them. Ruthven (1908) was the first student of this genus to associate the forms here dealt with as a natural group, but he recognized only three of the eleven forms which I consider, the material available to him being limited. It is noteworthy that each form recognized by Ruthven represents in the present scheme of classification a series of closely related races comprising a separate section or "group" within the artenkreis. It will be obvious from the following systematic accounts, wherein differences in habits and habitats as well as in correlated structural features are set forth, that this recognition of additional forms is based on more than a mere trend toward "splitting," that is, the naming of minor geographic variants, for which the modern systematist is so often criticized.

To justify its nomenclatural recognition as a distinct subspecies, a geographic race of *Thamnophis* must differ from all other races to the degree that every individual (except for geographic intergrades) may be identified by a student of the group. In other words, a population distinct enough to be recognized as a subspecies should also be distinct enough to justify its recognition as a species if it does not intergrade with neighboring populations. I do not consider degree of differentiation a valid criterion for distinguishing species from subspecies; the minimum differentiation which justifies the naming of a form should be the same for either species or subspecies, though of course species have often become differentiated to a degree seldom or never found between races of the same species.

It is not the purpose of this study to present an exhaustive account of the natural history of *Thamnophis ordinoides*. Collecting the data for such a study for even one of the subspecies here included would have necessitated further prolonged and intensive field work, perhaps extending over several years. Rather, it has been found necessary to concentrate on the two phases of the natural history which are most easily investigated, namely, habitat and feeding habits.

The purpose of the present report is thus twofold: first, to bring down to date the classification of *Thamnophis ordinoides,* a group so complex in its subspeciation that it has never been well understood by herpetologists although it has been revised twice in the last thirty years; second, to demonstrate the adaptive nature of subspecific or racial differences, with data based on observation of living individuals in their natural habitats as well as on preserved specimens.

ACKNOWLEDGMENTS

I take pleasure in expressing my gratitude for encouragement and assistance received from Professor Joseph Grinnell (since deceased), under whose guidance this research was carried out. The facilities afforded by the University of California Museum of Vertebrate Zoölogy, and the congenial coöperation of the staff and graduate students, have also assisted in the preparation of this work. At the Museum, Dr. Jean M. Linsdale, in particular, has given helpful suggestions and advice on the handling of statistical data.

For the loan of the collections under their care, and for many courtesies extended in the use of these collections, I am deeply indebted to each of the following persons: Dr. Helen Thompson Gaige, of the University of Michigan Museum of Zoölogy; Mr. Laurence M. Klauber, of the San Diego Society of Natural History; Dr. E. B. Shelley Logier, of the Royal Ontario Museum; Mr. Joseph R. Slevin, of the California Academy of Sciences; Dr. Albert W. Herre and Mr. L. Morgan Boyers, of the Stanford Museum of Natural History; and Dr. Arthur Svihla, of the Charles R. Conner Museum, Washington State College.

For important information on types and other specimens in the United States National Museum I am indebted to Dr. Leonhard Stejneger and Miss Doris Cochran. Dr. Howard K. Gloyd, of the Chicago Academy of Sciences, has very kindly supplied photographs of certain living garter snakes. Many of the photographs here included were taken by my father, Mr. Chester Fitch. My father and my brother, Mr. Chester Fitch, Jr., have made extensive collecting trips to obtain needed specimens. For this assistance I am grateful.

MATERIALS AND PLAN OF PRESENTATION

A total of 2823 specimens were examined in the collections just mentioned. I examined also all specimens in the collections of the Sacramento Junior College Department of Zoölogy and of Mesa Verde National Park, the private collection of Mr. Jack von Bloeker, Jr., and all material in the United States National Museum from the state of Nevada.

Of the eleven forms of this group, all but two (the lower Californian forms *hueyi* and *digueti*) were studied in the field. Approximately 850 specimens representing 150 localities were collected, and these were accompanied by field notes.

In their revision of western garter snakes, Van Denburgh and Slevin (1918) published individual scale counts for hundreds of specimens, including most of the material then in the California Academy of Sciences, Stanford University, and the Museum of Vertebrate Zoölogy. In general these data have been found to be accurate, though incompletely analyzed by the authors, and they have been freely used in the present paper. However, the specimens have been reëxamined and their identifications verified, and additional data have been recorded for nearly every one of them. My counts of preocular scales differ from Van Denburgh and Slevin's, especially in the race *biscutatus*, the disparity evidently arising from my different interpretation of observed characters. In dried-out or shrunken specimens the preocular is wrinkled, appearing to be divided when actually no suture is present; in other specimens, preocular plates are only partly divided by sutures. In my records two preoculars are counted only when a deep, well-defined suture completely separates upper and lower portions of the originally single scale.

Ordinarily, the minimum data recorded for each specimen include the number of preoculars, supralabials, infralabials, gastrosteges, and urosteges; head and body length, tail length, and points of appearance and disappearance of each longitudinal scale row present on the body but not continuous from head to anus. Other data recorded in a large proportion of the specimens include measurements of certain head scales (width of internasorostral contact, and of nasorostral contact on one side), measurement of posteroinferior angle of sixth supralabial, color of dorsal and lateral stripes, number, size, and shape of supralabial, wedge marks, presence or absence of red spots, presence or extent of ventral pigmentation, color of supralabials, presence and number of developing embryos in gravid females, and presence of knobs on keels of the scales of anal region in males.

Many of the specimens in the Stanford collection were identified on the basis of the more important structural features without recording of minutiae throughout. Decision to record certain structural features was made only after some borrowed specimens had been returned; and so such characters will not be found recorded for all specimens.

The synonymies given in this paper for each form are lists of all the scientific names which have been applied to that form, arranged chronologically. Color descriptions were made from living or freshly killed snakes (except for *hueyi* and *digueti,* of which no living individuals were seen). Names of colors which are capitalized are those of Ridgway (1912). Descriptions refer to typical specimens, each representative of the population at a type locality—a population which coincides with a "differentiation center" where subspecific characters are strongly developed.

In the original manuscript of this paper, now filed as a dissertation in the University of California Library, the itemized natural history data used as a basis for the summaries of habitats and feeding habits presented here were included *in extenso.* It was not practicable to publish these data in full, because of their bulk, but the original is available to anyone desiring more specific details. In the distribution maps, localities are shown only for specimens actually examined and identified by me, but I believe my material has been sufficient to show the approximate range of each form.

Ecologic groups within the artenkreis are discussed in separate sections, each of which immediately follows the accounts of its component forms. Ecologic differences and similarities between forms are therein discussed and correlated with structural features; also the general trends of variation throughout the group are traced, and statistical data for structural characters are presented in graphs, tables, and diagrams. In the arbitrary groupings of specimens uniformity has not been maintained throughout. An effort has been made to subdivide each form to a point where variation becomes mainly individual rather than geographic in the separate populations dealt with. For relatively stable characters, less subdivision is necessary than for those which are subject to much geographic variation; hence fewer and larger series representing fewer and larger geographic areas have been grouped together. In dividing populations, political boundaries have been followed in some measure for the sake of convenience, but an attempt has been made also to follow boundaries of faunal areas and to subdivide the artenkreis into homogeneous groups.

USE OF THE TRINOMIAL

Consistency has been sought in applying the concept of species and subspecies to the forms of this group. For several, however, it is doubtful whether the binomial designation, implying separate species, rather than the trinomial designation implying a geographic race, more appropriately expresses the facts. This doubt has resulted not so much from lack of material sufficient to disclose the true situation as from differences in treatment of parallel data in other groups of vertebrates by contemporary workers.

I quote the following opinions to illustrate the conflicting views of systematists. Merriam (1919:7) wrote: "To my mind the *criterion of intergradation* is one of the most pernicious that has ever been introduced into the systematic study of animals and plants.... *Is not the measure of relationship* of more consequence than the accident of survival or non-survival of intergrades?"

Grinnell and Hill (1936:9) expressed an opposing view when they stated that reliance should be placed on an objective criterion "—that of intergradation *demonstrated to exist* on the present time level—in determining whether to use for a given form, the trinomial rather than the binomial."

In general I adopt the criteria set forth by Grinnell and Hill as quoted above, but with the following reservations: When insufficient material is available for the demonstration of the actual geographic merging of two forms, ecologic similarities and continuity of habitat should be weighed in making a decision on their specific or subspecific ranking. When two forms, which replace each other ecologically in adjacent areas are similar in habits and differ only in minor structural characters, intergradation may be safely assumed and the forms should be considered subspecies if their habitat is continuous. However, if an obvious physical barrier intervenes between their known ranges, seemingly precluding the possibility of geographic intergradation, they should be accorded specific ranking, if sufficiently differentiated to justify the use of separate names.

It has been possible, wherever forms of garter snakes occupy adjacent ranges, to demonstrate either actual geographic intergradation or separation by a barrier. One form, *Thamnophis digueti,* isolated in the southern part of the peninsula of Lower California, and having peculiar characters, is recognized as a distinct species. Nevertheless, among birds and mammals, there are forms equally isolated from northern relatives, some of them perhaps having equally distinctive racial characters, which are accorded only subspecific ranking in current taxonomy. *Thamnophis hammondii* also is herein recognized as specifically distinct because it is isolated from other forms. Although it is separated from its nearest relative by only a few miles, and the two forms approach each other in characters where their ranges are adjacent, there is an actual hiatus in distribution and all specimens seen can certainly be allocated to one form or the other. A third isolated form, *Thamnophis ordinoides hueyi,* is classed as a subspecies because, although it is not connected with other races by continuous geographic intergradation, it is linked with the race *elegans* by a geographically and structurally intermediate isolated population. The entire group is thus an artenkreis consisting of two isolated species and a rassenkreis of nine races.

Even with definite concepts of the scope of the terms "species" and "subspecies," I have found the practical application of these terms difficult. This fact serves to illustrate the lack of any real, qualitative differences between them. It is probable that certain forms of the artenkreis would unhesitatingly be assigned to distinct species by some systematists, and that other workers would lump them all as subspecies. For each named kind, one or the other course has to be adopted even though some forms are truly transitional between the "species" and "subspecies" as I define them.

The geographic overlapping of subspecies in *Thamnophis ordinoides* is unusual, but it is not unique; parallel situations have already been demonstrated in several vertebrate species (or rassenkreise). Nevertheless, sytematists still commonly assume that when two closely related forms are found together in the same region their specific distinctness is demonstrated by the overlapping. It is probable that when the fallacy of this assumption is fully comprehended, certain overlapping forms now classed as separate species actually will be found to intergrade elsewhere, indirectly through intermediate races. Such subspecific overlapping could develop only in a widely distributed, geographically variable species, responsive to the varied ecologic situations under which it occurs, because of generalized and adaptable structure and habits. Another requisite is a potentiality for developing physiological, morphological, or psychological barriers to crossbreeding in its component races.

It seems probable that where two or more kinds of garter snakes occur together there is some competition between them. However, each form apparently differs in habits from every other, so that no two occurring within an area ever occupy exactly the same ecologic niche; otherwise, one would inevitably crowd out and replace the other.

There is no evidence of active or direct competition between garter snakes in the wild. Although different forms have often been collected within a few feet of each other, and dozens of individuals have been kept together in captivity, no trace of social intolerance or aggressive behavior toward one another has been observed. Ordinarily, individual garter snakes behave toward each other as toward inanimate objects. Therefore it appears that one form affects the fortunes of another only indirectly through its influence on the biotic factors of their common environment, particularly on the food supply. Probably there is no overlapping in food habits, and so no competition, between *hydrophila* and *ordinoides* where they occur together in southwestern Oregon. However, *vagrans* and *couchii* are similar though not identical in feeding habits, and interracial competition between them may be acute in the narrow belt where they overlap, in west-central Nevada and east-central California.

CHARACTERS USED IN CLASSIFICATION

Definition of the artenkreis.—The range of geographic and individual variation is so great within *Thamnophis ordinoides* that no character of scalation or coloration is at the same time common to the species as a whole and yet peculiar to it as contrasted with other forms of the genus. The range of variation within this artenkreis nearly equals that of the entire genus in some of its characters.

The scalation is typically colubrid. On top of the head the plates include a rounded rostral; a pair of quadrangular internasals which are sometimes longer than broad, and markedly narrower anteriorly than they are posteriorly; a pair of prefrontals; a frontal, bordered on either side by a supraocular; and large paired parietals. On each side of the head there are from 6 to 9 (usually 8) supralabials, and from 8 to 12 (usually 10) infralabials. The supralabials tend to be quadrangular and are bordered by the anterior and posterior nasals, the single loreal, the preocular (which may be divided into upper and lower portions by horizontal suture), the eye (in contact with 2 supralabials—the 4th and 5th when 8 are present), the lowest postocular, the anterior temporal, and the lower posterior temporal. There are usually 3 postoculars of approximately equal size arranged in vertical series. There is a single anterior temporal and 2 or 3 posterior temporals. The mental is triangular. The first pair of infralabials are in contact with each other medially behind the mental. There are two pairs of elongate genials; the members of the usually longer posterior pair are separated by small medial scales; those of the shorter anterior pair are in contact along the mid-line. There are from 184 to 137 gastrosteges and from 100 to 54 pairs of urosteges. The maximum number of scale rows on the body varies from 23 to 17, and the minimum (on the posterior part of the body) from 17 to 15. The dorsal body scales are keeled, except occasionally those of the lowest row on each side. The anal plate is undivided. The pupil of the eye is round.

The color pattern consists typically of a dark dorsal ground color with a median dorsal stripe and a pair of lateral stripes. The dorsal stripe is usually widest near its anterior end, and may cover three scale rows, or it may be confined to the middorsal row, or be absent; it is usually some shade of yellow, but may be orange, bright red, or pale brown. The lateral stripes are on the second and third scale rows on each side and are usually pale yellow, often suffused with dusky color, but they may be red; in *digueti* and in some individuals of other races they are absent. Between the dorsal and lateral stripe on each side, two alternating longitudinal rows of dark spots are superimposed on the usually paler ground color. Behind each spot are several pale flecks of a yellowish, greenish, or bluish tint, mainly restricted to the skin between the scales. The ventral surface is usually pale yellowish gray, with a pinkish suffusion posteriorly. Each gastrostege usually has a black spot near its anterolateral corner on each side. The supralabials are usually pale, with sharply defined black markings along their posterior edges. Among these marks, one is typically broadest at its upper end and tapers to a point below. Because of this wedge shape, such marks are referred to in this paper as "supralabial wedge marks." The gastrosteges may be heavily marked with black or red or yellow. Yellow parietal spots are usually present.

Adult males differ from females in several respects. They are smaller, on the average; have more gastrosteges and urosteges, or more shortened scale rows; sometimes have sensory pits on certain of the head shields, which may include the rostral, internasals, prefrontals, several of the anterior labials, the mental, and the genials; knobbed keels are present on scales of several of the lower rows in the anal region of the body and tail; the tail is longer, and relatively thicker at its base.

The hemipenis usually extends to the 14th urostege (13th to 17th); it is simple, not forked or lobed. The sulcus is unbranched, with two large basal spines on its medial side, the proximal one being slightly the larger. Of the three basal spines on the lateral side of the sulcus, the distal one is largest, the middle one is less than half as large and is set farther laterad, and the basal one is nearly as large as the outer, but slightly more curved. The basal spines are recurved and compressed, and fleshy nearly to the tips; all five are confined to the basal third of the hemipenis. Distal to the basal spines the entire organ is studded with minute recurved spinules which are arranged more or less in oblique rows and gradually decrease in size toward the distal end. The individual spinules are well separated. There are no calyces, flounces, lamellae, or papillae. The lips of the sulcus are not prominent.

Type of variation.—Study of the variation within this group has impressed me with the futility of attempting to show geographic differentiation with a limited number of predetermined standardized characters. Certain characters which are stable throughout most of the range vary greatly within limited areas. Variation in populations parallels variation in environment so closely that no two populations have the same combinations of characters. Only those characters which were observed to vary were recorded. Many variable characters were not readily treated statistically.

The characters recorded may be grouped under the separate headings of scalation, size, coloration, and proportions. Scale characters used include number of certain head scales (preoculars, supralabials, infralabials); numbers of scale rows on body, and lengths of certain of these rows, the 5th, 6th, 4th,

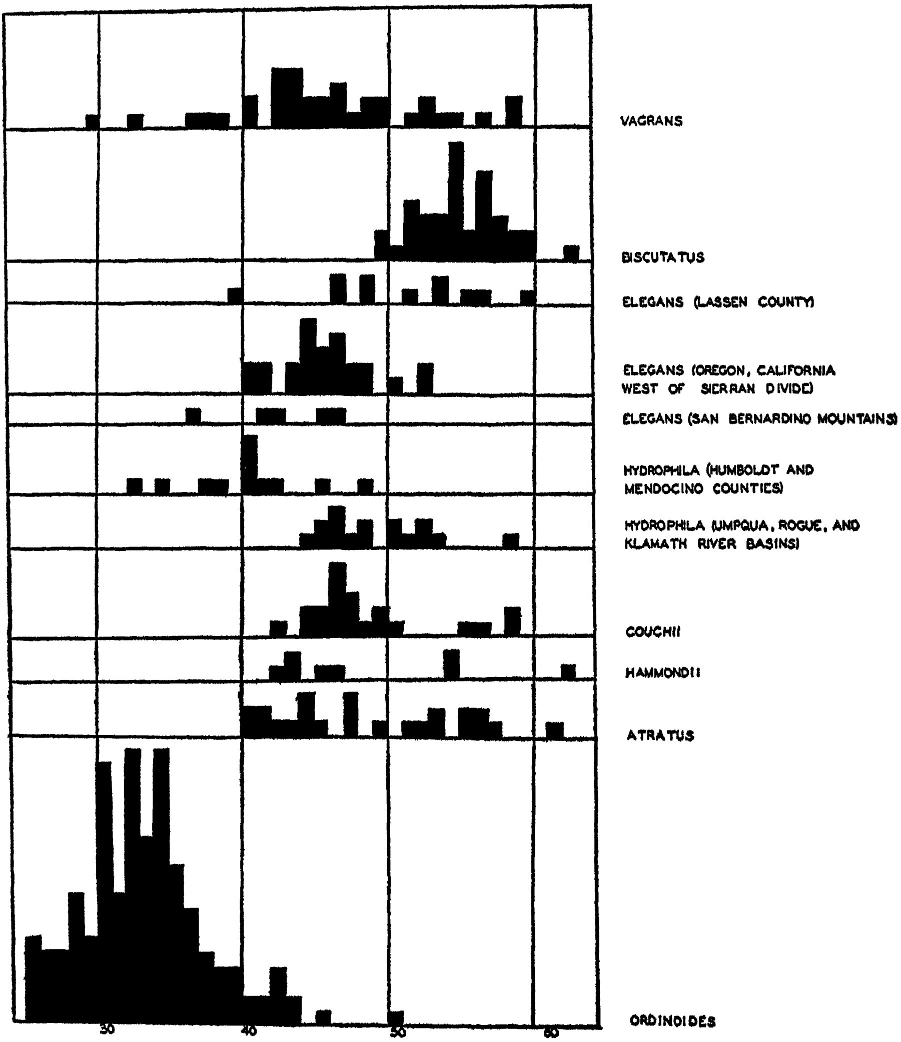

Fig. 1. Histograms showing head and body lengths in centimeters of adult males of *Thamnophis ordinoides.* Each square represents a specimen. In forms other than *T. o. ordinoides,* only specimens having knobbed keels on the scales of the anal region are included (on the assumption that males not showing this character are immature). In *T. o. ordinoides,* however, all males longer than 24 cm. are included since none has knobbed anal keels well developed in this subspecies. Note that *biscutatus* is much larger than typical *elegans,* and that intergrading populations of Lassen County are of intermediate size; that the southern population of *elegans* in the San Bernardino Mountains is small; that *hydrophila* is smaller in the coastal region than in interior valleys; that *ordinoides* is much smaller than the other forms; that, in general, males are smaller than females (compare fig. 2).

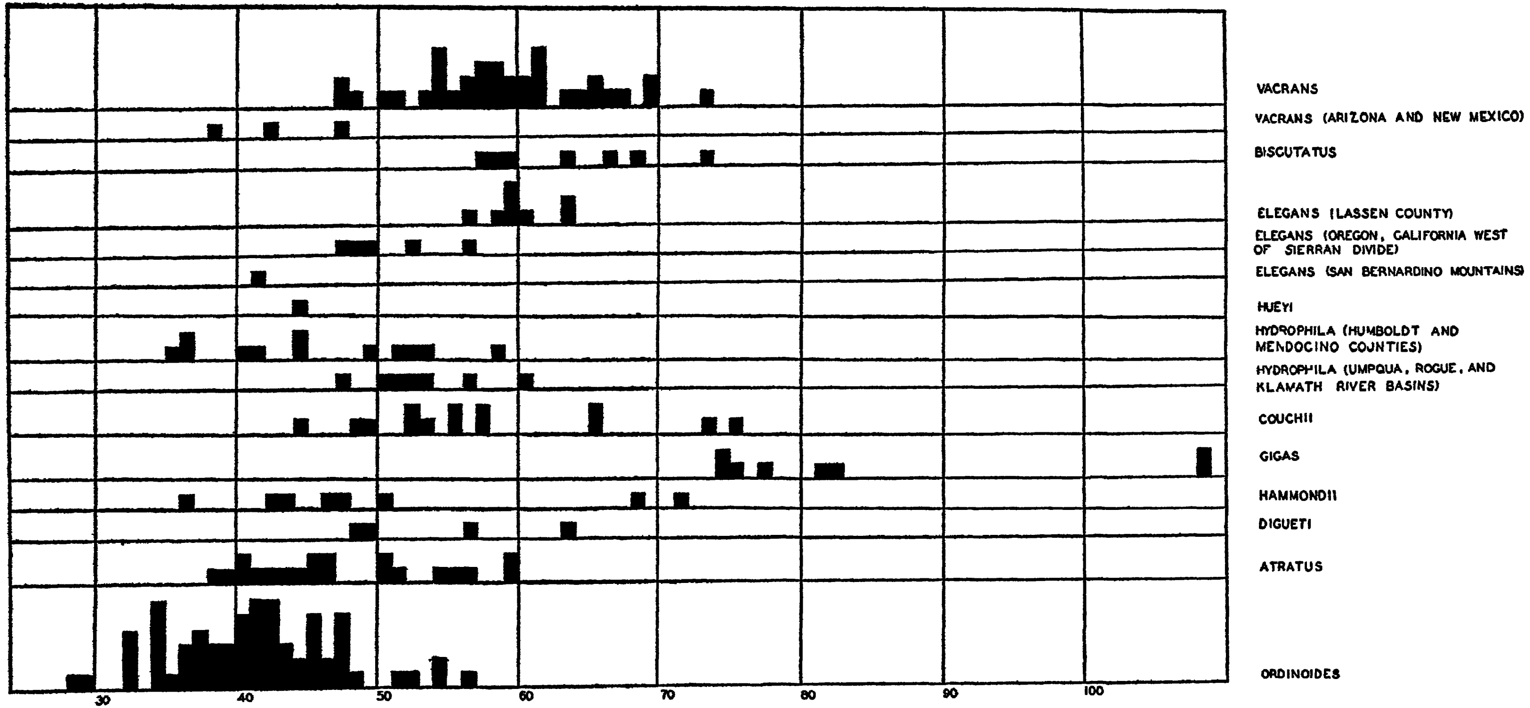

Fig. 2. Histograms showing head and body lengths in centimeters of adult females of *Thamnophis ordinoides*. Each square represents a specimen. Only females containing developing ova (hence sexually mature) are included. Note that both *vagrans* and *elegans* are smaller at the southern end of their ranges than elsewhere; that *hueyi* resembles southern populations of *elegans* in being of small size; that *biscutatus* is relatively large; that *gigas* is larger than any of the other forms; that *ordinoides* is markedly smaller in average and maximum size than any of the other forms; that adult females are, in general, larger than adult males (compare fig. 1); that reduction in size is correlated with reduction in numbers of gastrosteges and relative lengths of scale rows.

and 7th of the original 23 expressed as percentage of the head and body length; the percentage of the anterior genials to the posterior genials; the percentage of the contact of the nasal with the rostral to that of both internasals with the rostral; the posteroinferior angle of the 6th supralabial Characters of the color pattern which were found to vary geographically include shade of ground color on head and body; shades of dorsal and lateral stripes and their extent; color of iris; facial markings, including shade of supralabials; size and shape of supralabial wedge marks and temporal bar; development of parietal spots; size and shape of dark dorsolateral spots on body; size and color of flecks on dorsolateral area; general coloration of ventral surface and extent of suffusion with pink, purple, or ochraceous coloring; extent of black, yellow, or pink markings. Characters of body proportions include diameter of body, width of head, shape of muzzle, relative size of eyes, and relative length of tail. Characters of body proportions vary ontogenetically as well as geographically and some of them are of a secondary sexual nature. In embryos and young of garter snakes the head is large in proportion to the body; likewise the eyes are large in proportion to the head. As the animal grows, the proportions of these parts gradually change. Despite this ontogenetic variation, the same characters—for example, large size of eye in *hammondii* and narrow head in *ordinoides*—contribute in large measure to produce the peculiar and distinctive appearances of these forms, and thus also show geographic variation.

Number of gastrosteges.—This was found to be the most valuable single character used to show geographic variation within the species studied. It is not influenced by age or condition of the specimen. Marked sexual dimorphism in numbers of gastrosteges necessitates handling the data for the two sexes separately, and in reducing by half the number of individuals within each series it reduces the reliability of the averages. However, approximately the same difference may be expected between the sexes in each series, so that the results obtained for one sex serve to verify the figure obtained for the other. The most closely related races usually differ markedly in numbers of gastrosteges. Some forms differ from others to such a degree that no overlapping can be shown, even between extreme individuals in large series; most of the subspecies overlap in this character, but they show average differences. Even within single subspecies, geographic populations which are closely similar in other respects show average differences in this character.

In most of the larger series (as segregated in diagrams, figs. 3, 7, 13, and 18) the standard deviation was between 3 and 4, though in a few series more than 4 and occasionally less than 3 (notably in those representing single localities, such as the large Klamath Falls series of *biscutatus*). The small numbers of specimens in most of the series used makes the value of the standard deviations questionable, but if these series were combined their standard deviation would be much higher, and would be determined mainly by geographic rather than individual variability.

Numbers of urosteges.—The remarks on gastrosteges apply here also (see figs. 4, 8, 14, and 19). However, frequent injuries to the tail reduce the number of specimens that may be used, and the number of urosteges is correspondingly less reliable than the number of gastrosteges. Such injuries often are not easily recognized and there is danger of including specimens lacking a few of the terminal urosteges. Sexual dimorphism here is more marked than in the number of gastrosteges, but in general the two characters parallel each other closely in geographic trends.

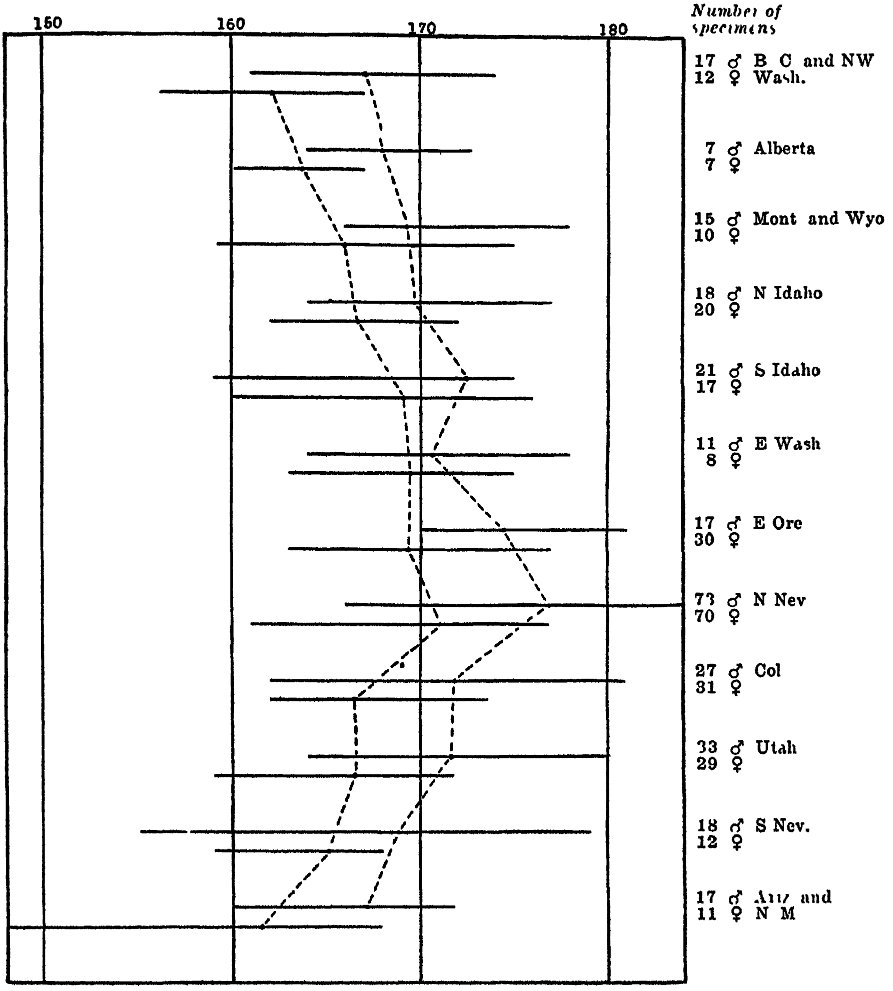

Fig. 3. Numbers of gastrosteges in populations of *Thamnophis ordinoides vagrans*. Sexes are plotted separately. Dotted lines connect the means of each series. Note the high number of gastrosteges in that part of the range which is latitudinally central, and the progressive decrease in populations nearer the northern and southern extremes of the range. Idaho specimens are divided into northern and southern groups, the former from the Rocky Mountain area, the latter from the Great Basin area. "Southern Nevada" specimens include those from Esmeralda, Nye, and Lincoln counties; "northern Nevada" specimens are those from all more northern counties.

Length of body scale rows.—Former students of the genus *Thamnophis,* notably Cope, Ruthven, and Van Denburgh, have used the number of scale rows on the body as a character distinctive of the different forms. Because the scale rows do not always run continuously from the head to the posterior end of the body, it was necessary to record the number at different points along the body. Thus the formula 19–21–19–17 was used to indicate that on the anterior part of the body 19 rows were present, that farther posteriorly another row was added on each side, but that even farther posteriorly the number was reduced to 19 again, and to 17 at the end of the body. Ruthven (1908 :16–21) discovered that the rows drop out in a definite sequence; 23 is the maximum number for the genus *Thamnophis*, and when this number is present on the anterior portion of the body, it is the 5th row above the gastrosteges on each side which first becomes suppressed. The 6th, 4th, and 7th rows of the original 23 drop out in the order named. Toward the end of a row the scales become

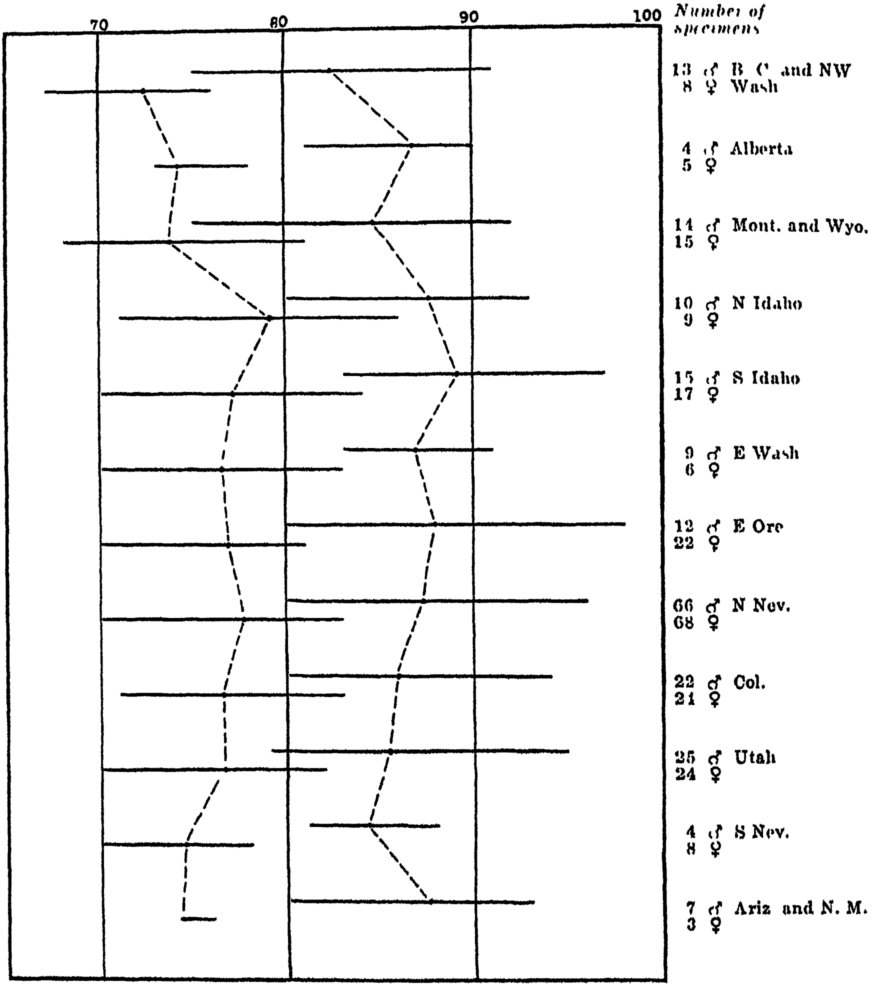

Fig. 4. Numbers of urosteges in populations of *Thamnophis ordinoides vagrans*. Note that there is a slight tendency toward reduction of these scales toward northern and southern extremes of the range, corresponding to trends in numbers of gastrosteges, but that the variation is much less marked than in numbers of gastrosteges.

small and crowded and finally disappear, and the scales of the adjacent rows on either side enlarge to fill the remaining space. Sometimes a row is discontinuous toward its end, and one or more isolated scales are separated from others of the same row. When a row is present for only a short distance on the anterior portion of the body, it is likely to be overlooked altogether unless special search is made. The length of each of the variable scale rows was measured on both sides of the body in most specimens. Since the total head and body length of every specimen was also recorded, the length of the scale row is expressed as a percentage of it. There is a tendency toward sexual dimorphism (see p. 46); in males the length and average number of scale rows are reduced as compared with females. This dimorphism is slight in proportion to the geographic variation. Individual variation is great in some populations which are tending to lose certain scale rows, the difference sometimes amounting to an entire row in specimens from a single locality.

Quotation marks are used with the number of a scale row to indicate its position with relation to other rows of the full complement of 23, thus expressing homology irrespective of the number of rows present in the individual specimen. The "7th" row would, however, actually be the 6th in a snake which lacked the original "5th" or would be the 5th in a snake which lacked both the "5th" and "6th" of the original 23. Such a snake would possess only 19 rows, having lost 2 rows on each side.

The "7th" row, if it is reduced at all, is shortened from the posterior end only and not on the anterior portion of the body, where 17 is the minimum number of rows. The "4th," "6th," and "5th" rows are often shortened anteriorly as well as posteriorly. These all center at a point approximately 30 per cent of the distance from the tip of the snout back to the anus; it is at about this point that the maximum number of rows generally occurs. If a row is more than 60 per cent of the head and body length, it is usually not reduced at the anterior end, but if less than 60 per cent, it is, on the average, shortened about equally on both ends, from a point approximately one-third the distance from the head back to the anus.

Number of supralabials and infralabials.—There are normally 8 pairs of supralabials in all the subspecies except *ordinoides*, which usually has 7 pairs, and rarely 6 or even fewer. Each form shows occasional departures from the normal number of 8, usually as a reduction to 7, rarely as an increase to 9. These tendencies represent slight average differences between the subspecies. When the number of supralabials is reduced to 7, this is usually effected by a fusion of the original 3d and 4th (see Ruthven, 1908:23). In those snakes which have 7 supralabials, the 3d and 4th border the eye below; in those having 8, the 4th and 5th border the eye. When 9 supralabials are present, the additional plate is intercalated between the 3d and 4th of the original 8, so that the 5th and 6th are in contact with the eye. Occasionally two or more of the supralabials behind the eye are fused, but this is an abnormal condition. The number of supralabials often differs on the two sides of the head; however, there is a strong tendency to preserve bilateral symmetry. Abnormalities, such as small supernumerary intercalated scales, or partial closing up and obliteration of a suture, are likely to be the same on the right and left sides of the head.

Ruthven (*loc. cit.*) showed that the maximum number of infralabials in *Thamnophis* is 11 on each side, and that numbers 5, 4, and 10 are lost in the order named. Ten is the normal number of infralabials in all members of the *Thamnophis ordinoides* artenkreis except *couchii*, which usually has 11 in the northern part of its range, and *ordinoides*, which has only 9 or 8.

Number of preoculars.—The paired preoculars usually are single on each side of the head, but in certain forms they show strong tendencies to division by horizontal sutures into upper and lower portions on each side. Though the divided preocular is not constant in any race, it is found in the majority of individuals of *hammondii* and *digueti*, and in a large proportion, though less than half, of specimens of *ordinoides* and *biscutatus*, and occasionally in other forms. It is a useful taxonomic character, since in several closely related races individuals differ in average numbers of preoculars. The forms having the preoculars divided do not constitute a natural group, but instead may be only distantly related, as this tendency appears within each of the three main groups which compose the artenkreis.

Size.—Among reptiles generally there is little uniformity in the size of adult individuals of a given species. Growth continues after breeding maturity is attained, and, to some degree, throughout life. Reptiles grow slowly, and it is often impossible to determine whether an individual is adult. Systematic workers in herpetology have therefore mostly disregarded size as a character of subspecific value.

It is evident that there is geographic variation in size among populations of *Thamnophis ordinoides*, because certain populations so far differ from others that no overlapping occurs between sexually mature individuals of the same sex. Comparative measurements indicate that each subspecies differs from the others, and that within each wide-ranging subspecies there is significant geographic variation in size. A large proportion of the specimens examined were immature, and therefore not available for a study of this character. Among females, maturity can be safely assumed only when the oviducts contain developing ova or embryos, and many adult females were not breeding. In males the presence of knobbed keels on scales of the anal region has been in general relied upon as indication of adulthood. However, this character may be influenced by individual variation, and it is lacking in some sexually mature individuals. In one subspecies (*ordinoides*), of which abundant material was available, not even the largest and (presumably) oldest males have this character well developed. Probably other races differ in the degree to which this secondary sexual character develops or in the stage of ontogeny at which it appears; nevertheless, when present it probably indicates adult size.

With these limitations, relatively few individuals can be used to show size differences, and the possibility of error is large. The material is not sufficient to show accurately the amount of difference, but is sufficient to show that differences exist. It also shows that those subspecies which are wide ranging are more variable in size than those which are restricted in range. This geographic variation may of course be partly environmental rather than genetic. In localities where food is abundant and the growing season is long, it might be expected that much larger average size would be attained than under less favorable conditions, even though populations are genetically the same.

In every series including numbers of adult specimens, the largest ones are females. Females attain much larger adult maximum and average sizes than do males, and there may be even greater disparity in minimum sizes of breeding adults.

Thickness of body.—Certain races appear to be more slender bodied than others. This difference cannot be well expressed in terms of the diameter measurement of the body, which varies widely according to the method of preservation—whether injected or not—and the condition of the specimen. The width of gastrosteges does not vary from these causes, since the scales themselves are not elastic; only the skin between them is capable of stretching. Also, it might be expected that increased thickness of body would be accompanied by increase in breadth of gastrosteges. Widths of gastrosteges were measured by peeling off the thin outer epidermal layer of one scale near the middle of the body, flattening it on a plane surface, and measuring from one corner to the other. This character was used to express differences in thickness of body between *elegans* and *biscutatus*, by taking the ratio of the width of the gastrosteges to the total head and body length. Only specimens whose total head and body length had been measured in the field were employed; in others, varying methods of preservation made this ratio unreliable. Though *biscutatus* was found to have wider gastrosteges, on the average, the difference was smaller and less constant than had been expected; probably the relatively thicker body in *biscutatus* is compensated for mainly by the larger number of dorsal scale rows and the areas of loose skin between the scales on the dorsal surface.

Internasorostral contact.—Each internasal may taper anteriorly, and thus have only a short anterior side in contact with the rostral, or it may be broadly truncate, in correlation with the shape of the muzzle. Forms with a blunt muzzle have broadly truncate internasals; those in which the muzzle is more elongate and pointed have longer, tapering internasals. Below the internasal on each side, the nasal is broadly in contact with the rostral; size and shape of the nasal do not vary appreciably in different forms. Variation in shape of the internasal, reflecting variation in shape of muzzle, is thus best expressed by the ratio

$$\frac{\text{width of combined contact of both internasals with rostral}}{\text{width of contact of left (or right) nasal with rostral}}$$

This ratio is usually more than one in forms with blunt muzzles and broadly truncate internasals (*elegans, hueyi, atratus*), and less than one in forms with long pointed muzzles and more tapering internasals. There is great individual variation in this character. Also, the percentage of error in recording measurements is large because of the small size of the parts measured and the occasional distortion of head shape in preserved material. For these reasons the averages for populations cannot be considered highly accurate, but they do show the general trends of variation within groups and the approximate differences.

Length of genials.—Of the two pairs of genials the posterior pair is generally longer, but the ratio varies in different forms. In *T. hammondii* the greater length of the posterior genials is conspicuous; in *elegans* and *atratus* the genials of anterior and posterior pairs appear to be of approximately equal length, especially since the anterior ends of the posterior pair are overlapped by the anterior pair. Differences between populations in length of genials have been shown by comparing the ratio of length of the anterior genial to length of the posterior one. Frequent fusion of one or more of the genials with other scales, abnormality in shape, or splitting into two or more separate scales results in a wide range of variation in this character within each series. Because of their small size and flexibility, these scales cannot be measured with a high degree of accuracy. Nevertheless, the averages and extremes obtained for different populations show that significant differences exist, and that general trends of variation can be traced throughout the entire group.

Posteroinferior angle of 6th supralabial.—In certain forms those supralabials which are posterior to the eye are enlarged and swollen in appearance, whereas in others the same scales are relatively small, mainly because of the reduced size of the underlying salivary glands. This decrease in size of supralabials is accompanied by changes in their shape; usually the sutures separating them are less nearly vertical and slant obliquely forward. Changes in size and shape are especially noticeable in the 6th supralabial (of the usual 8) when different forms are compared. To express these differences, measurement of the angle of the lower hind corner of the 6th supralabial was made after peeling off the thin epidermal layer of this scale and flattening it on a plane surface. The angle was measured by plotting three of the four corners of the scale, the posterior and inferior ones, with the lower hind corner forming the apex. Only average differences could be shown with this character, since the range of individual variation is large. There are marked differences in curvature of the sutures between supralabials, but these are not shown by the method used.

Thamnophis ordinoides vagrans (Baird and Girard)

(Wandering Garter Snake, Green Garter Snake, Great Basin Garter Snake)

Eutaenia vagrans Baird and Girard, 1853:35 (original description)
Eutainia vagrans, Lord, 1866:306
Eutaenia vagrans vagrans, Yarrow, 1875:551
Eutaenia vagrans plutonia Yarrow, 1883:152
Eutaenia Henshawi Yarrow, 1883:152
Eutaenia elegans lineolata Cope, 1892:655 (part)
Eutaenia elegans vagrans, Cope, 1892:656 (part)
[?] *Eutaenia sirtalis vagrans*, Taylor, 1892:325
Tropidonotus vagrans, Boulenger, 1893:202
Thamnophis vagrans, Stejneger, 1893:213
Natrix valida valida, Cope, 1900:984 (part)

Eutaenia elegans vagrans, Brown, 1903:290 (part)
Thamnophis ordinoides elegans, Ruthven, 1908:138 (part)
Thamnophis elegans, Cockerell, 1910:131
Thamnophis ordinoides vagrans, Van Denburgh and Slevin, 1918:240
Thamnophis ordinoides couchii, Erwin, 1925:7

Type.—Adult female, U. S. Nat. Mus. No. 907, collected in "California" [=southwestern Utah ?] by Wm. Gambel.

Range.—Great Basin and Rocky Mountain regions of the western United States, from extreme northwestern Oklahoma, New Mexico (except southern and eastern parts), northern Arizona, and the high Sierra Nevada of Tulare County, California, north on to Vancouver Island and the Olympic peninsula in Washington, and to Banff and Rocky Mountain Park, Alberta; east to the Black Hills region of South Dakota; in Oregon confined to regions east of the Cascade Mountains and east of the Klamath Lake basin; does not occur in northern California (see fig. 5).

Diagnosis.—Maximum number of scale rows on body usually 21, all extending posteriorly to mid-body; supralabials 8, 8 (sometimes reduced to 7); infralabials 10, 10; gastrosteges more than 147; urosteges more than 67; ground color brown, often pale brown or tan; dorsal stripe present for full length of body; dull, yellowish or brownish, suffused with dusky color; supralabials dull, brownish, approximating ground color of body; posterior supralabials enlarged and of swollen appearance; suture separating 6th and 7th supralabials nearly vertical, not convex posteriorly; iris heavily pigmented, with narrow, paler yellowish rim around pupil; black spots on body small and well separated, those of upper rows on each side tend to invade edges of dorsal stripe, or even to break through it and join medially; labials sometimes finely dotted with black; ventral surface marked with black medially, often in extensively continuous areas; head large, distinct from neck; eyes relatively small.

Coloration.—Description of living adult female collected at Cline Falls, Deschutes River, Deschutes County, Oregon.

Top of head Light Drab, Cinnamon Drab on internasals and prefrontals; supralabials between Light Drab and Drab-Gray, the last three edged with black superiorly, but with no wedge marks developed along their posterior edges; scales of occipital region Cinnamon-Drab; temporals edged with black along contacts with supralabials; iris dark brown, clouded with pigment, but with narrow unpigmented golden-yellow rim bordering pupil; dorsal stripe ill defined, indistinct on posterior part of body, better developed anteriorly, its scales shading from Yellow Ocher to Buckthorn Brown, edged with Picric Yellow on anterior part of body; ground color Drab; lateral flecks Yellowish Glaucous, mainly confined to skin between scales but encroaching on edges of scales; centers of scales lying within dorsolateral spots Cinnamon-Drab; lateral stripe Vinaceous Buff with a faint ochraceous suffusion; first row of scales above gastrosteges Light Drab; chin and first six gastrosteges immaculate white; posteriorly gastrosteges gradually become dusky, Pale Drab-Gray for most of body length, becoming darker, near Drab-Gray on tail; one black spot on each anterolateral corner of each gastrostege; anterior half of each gastrostege finely dotted with black except at anterior end of body; posterior gastrosteges and urosteges tinted with Buff Pink on their median portions; posterior urosteges almost entirely Buff Pink.

Comparisons.—*T. o. vagrans* intergrades with the races *biscutatus* and *elegans*; its range overlaps the ranges of *couchii* and *ordinoides*. Comparisons with *biscutatus*, *elegans*, and *couchii* are made under the respective headings of those subspecies.

T. o. vagrans, as contrasted with *ordinoides*, has the dorsal stripe dull yellow, brown, or gray, rather than bright yellow, red, or orange; ground color brown, never black, gray, or reddish; head markedly wider than neck and distinct from it, as opposed to narrow head of *ordinoides*; gastrosteges nearly always more than 150; urosteges more numerous on the average; infralabials 10 pairs rather than 9 or 8 pairs; supralabials 8 pairs rather than 7 pairs; maximum number of scale rows on anterior part of body 21 rather than 19 or 17; size larger (see p. 8).

Remarks on nomenclature and systematics.—The type specimen of *T. o.*

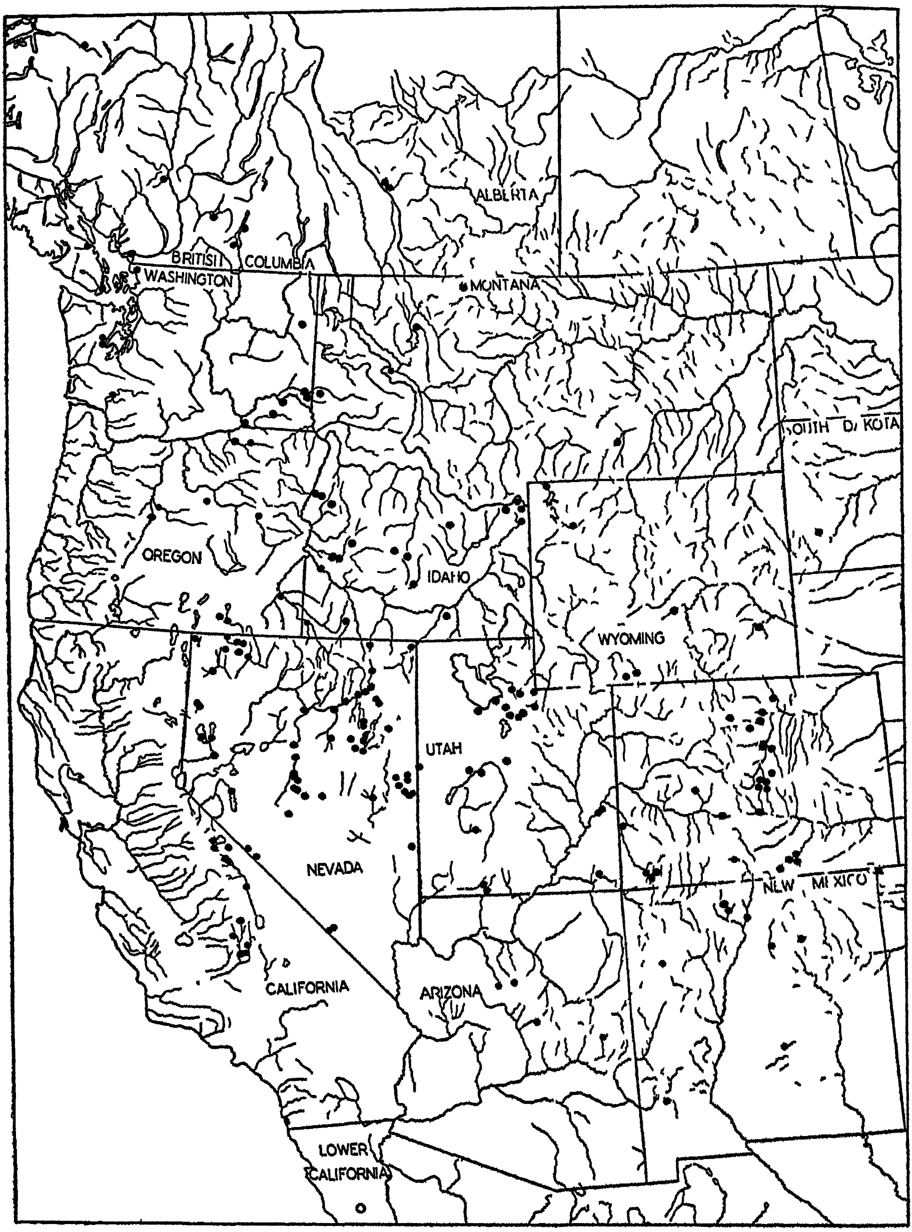

Fig. 5. Distribution of *Thamnophis ordinoides vagrans* (dots represent specimens examined) in western North America, and of *Thamnophis ordinoides hueyi* (circle) in northern Lower California, Mexico.

vagrans was stated to have been collected in "California" by Dr. Wm. Gambel. However, it seems improbable that this specimen was taken within the present boundaries of California, because the range of *vagrans* within the state is restricted to the high Sierra Nevada and to southern Mono County. I can find no record of Gambel's travels within California, but it is known that he came by way of the old Spanish Trail which crosses extreme southern Nevada and southern California entirely south of the range of *vagrans* (Brewerton, 1930:7). In Gambel's papers on the birds of California (1843:259–262, and 1846:44–48, 110–114, 154–158) all remarks pertain to species of the western part of the state or those of the southwestern deserts, and I can find no evidence that the author traveled in the Sierra Nevada. Therefore it seems most probable that the type of *vagrans* was collected in southwestern Utah. It is definitely known that Gambel passed through the range of *vagrans* there, and at the time of his travels that region was within the vaguely defined boundaries of "California," which was not then delimited to its present confines.

Three other specimens are mentioned in the original description, one from "Humboldt River, California" [=Nevada ?], one from south of Rio Grande, New Mexico, and one from Puget Sound. It is possible that the Humboldt River specimen actually came from California in the region of Humboldt Bay, and belongs to the subspecies *hydrophila,* which resembles *vagrans* in appearance Another specimen not seen by me (U. S. Nat. Mus. No. 901) but recorded by Cope (1900:1041) from "Humboldt Bay, California," is almost certainly *hydrophila* if the locality is correct.

Ruthven (1908:138) did not recognize *vagrans* as distinct from *elegans.* Van Denburgh (1897.212; 1922·837) and Brown (1903 291) incorrectly classified specimens of this subspecies from the Pacific Coast as *biscutatus*

Geographic variation and intergradation.—Throughout most of its range *vagrans* shows uniformity in the number of scale rows. Rarely a short "5th" row is present on the anterior part of the body, making a total of 23 rows as in *biscutatus.* Frequently several scales of the "6th" row are missing in the neck region. No definite geographic trends in these characters can be demonstrated except in specimens from the extreme northwestern part of the range, which tend to have the "6th" scale row reduced. The numbers of gastrosteges and urosteges show definite geographic trends which closely parallel each other, the maximum numbers occurring in snakes of northern Nevada and southeastern Oregon, a region centrally situated in relation to the range as a whole. To the north and south there is progressive decrease, with minimum numbers in the extreme southern part of the range in Arizona and New Mexico, and in the extreme northwest in British Columbia and northwestern Washington. The largest specimens were generally from the central part of the range, where numbers of gastrosteges and urosteges are relatively high, whereas the smallest adult specimens were from the northern and southern extremes of the range. Reduction in the number of gastrosteges and urosteges is apparently correlated with a dwarfing of body size, and both occur in peripheral parts of the range.

Throughout most of its range *vagrans* has undivided preoculars, but in the region of Vancouver Island and about Puget Sound the preoculars are usually divided.

Although *vagrans* shows relatively little geographic variation in color pattern, certain trends are noticeable. In the northwestern portion of its range the same population which departs from the typical condition in numbers of gastrosteges, urosteges, and preoculars, as shown above, is also peculiar in color-pattern characters. The ground color is darker brown than in typical *vagrans*. The dorsolateral black spots tend to be subdivided and are small and crowded. Ventral pigmentation is heavy, and often the posterior part of the body is nearly solid black ventrally. In specimens from Vancouver Island the dorsal stripe is better defined, and brighter yellow than in typical *vagrans*, but in those from the mainland of British Columbia it is faint. In all specimens from British Columbia the muzzle is blunter and wider than in typical *vagrans*, and the head appears to be narrower posteriorly and less distinct from the neck. The humid coastal area occupied by this population is faunally distinct from the rest of the range occupied by the subspecies. However, the incipient racial differentiation does not seem to me great enough to warrant its separation as a subspecies distinct from *vagrans*.

Shade of ground color, distinctness of dorsal stripe, and amount of black on top of head and on ventral surface are characters which show much variation, but this is mainly individual rather than geographic. Even among young of the same brood some may have continuous areas of black over most of the ventral surface, whereas others have only a few scattered dots of black. In occasional specimens from almost any part of the range, ventral pigmentation is nearly or entirely lacking, although others from the same or near-by localities may be heavily pigmented ventrally. Specimens from western Nevada often have the ventral pigmentation reduced to scattered dots and seldom have broadly continuous areas of black. This reduction in ventral pigmentation in the western part of the range may represent a tendency toward *elegans*, which seldom has extensive black markings on the ventral surface.

In spite of the obviously close relationship between *elegans* and *vagrans*, intergrading specimens are few and are all from a relatively narrow belt between the ranges of the two forms in western Nevada and east-central California. Two from Lost Creek, Washoe County (Univ. Mich. Mus. Zoöl. No. 78045) have the dorsal ground color of intermediate hue, darker brown than in typical *vagrans*. They have supralabials of pale color only slightly suffused with the buffy ground color, and bearing wedge marks as in *elegans*. Black on top of the head is less extensive than in *elegans*, being mainly confined to the parietals, supraoculars, and posterior portion of the frontal, and marbled with brown; the internasals, prefrontals, and anterior portion of the frontal are buffy brown. The gastrosteges are dotted with black medially. In each the dorsal stripe is bright yellow with no noticeable brownish suffusion, but of irregular outline.

Univ. Mich. Mus. Zoöl. No. 78044 from Grass Valley Creek, Washoe County, has the dorsolateral area dark brown, approaching the nearly black ground color of *elegans;* the dorsal stripe is distinctly yellow, with only a faint brownish suffusion; supralabial wedge marks are well developed, as in *elegans;* the ventral surface is heavily dotted posteriorly; the top of the head is light brown posterior to the anterior edge of the frontal; the frontal and supraoculars are heavily marbled with black, and the parietals are nearly solid black.

Two (Univ. Mich. Mus. Zoöl. No. 78042) from the Black Rock Desert, Humboldt County, Nevada, resemble typical *vagrans* except that the dorsolateral area is darker and the dorsal stripe brighter, of pale yellow with but little brownish suffusion. In these characters they seem to tend toward *elegans.*

All the intermediate specimens mentioned above approach *vagrans* more closely than *elegans* in their characters. Series from Smoke Creek in the vicinity of the California-Nevada state line, and nine miles east of the state line, are perhaps on the whole nearer to *elegans,* but they are intermediate and approach *vagrans* in having the dorsal stripe suffused with brownish color, the supralabials dusky, the dorsal ground color dark brown rather than black, the ventral surface marked with black, the body stockier than in typical *elegans,* and the size larger.

Specimens from the vicinity of Reno are nearest *elegans* but are less slender than typical *elegans,* their dorsal ground color is dark brown rather than black, and the parietal, frontal, and supraocular plates are marked with brown. One from "Camp 12," Truckee River, and others from Pyramid Lake are typical *vagrans,* indicating that intergradation takes place abruptly a short distance east of Reno. Mus. Vert. Zoöl. No. 6085 from Mono Lake Post Office is typical of *vagrans,* but other specimens from the vicinity of Leevining are nearer *elegans* in coloration. Most of them tend toward *vagrans* in having brown on the frontal, supraoculars, and parietals, and in having the ventral surface heavily marked with black. A female from this locality nearly typical of *elegans* in coloration gave birth to a brood of young all of which resembled her closely.

A specimen from Walker Lake, Mono County, California (Mus. Vert. Zoöl. No. 5958) and another from Owens Valley, Inyo County, California (Univ. Mich. Mus. Zoöl. No. 78065) are intermediate between *vagrans* and *elegans.* They show resemblance to *vagrans* in the brownish suffusion of the dorsal stripes, brown ground color, and heavy black markings on the ventral surface.

It is noteworthy that most of these intergrading specimens represent populations in small isolated drainage basins. Perhaps continuously interbreeding populations connect the two subspecies only in a few limited areas. Throughout its entire range the subspecies *vagrans* is separated into populations confined to isolated drainage basins by extensive areas of uninhabitable desert. The uniformity of characters throughout such populations is striking, especially since some of them must have been long isolated.

Specimens from the Warner Lake region of Lake County, Oregon, and Modoc County, California, are intermediate between *biscutatus* and *vagrans.* Univ. Mich. Mus. Zoöl. No. 78068 from Twenty-mile Creek, just above Warner Lake, Lake County, Oregon, has a uniformly brown dorsolateral area with small, inconspicuous black spots; the dorsal stripe is distinct and yellow but with a slight brownish suffusion. The supralabials are brownish. Other specimens from Deep Creek near Adel, Lake County, Oregon, and from Twelve-mile Creek, Modoc County, California, are similar in appearance. Mus. Vert. Zoöl. No. 21527 from Diessner, extreme northwestern Nevada, is nearer *vagrans;* it has a less distinct dorsal stripe and paler ground color than specimens from Twelve-mile Creek, which it resembles closely.

Specimens from Borax Lake (Univ. Mich. Mus. Zoöl. Nos. 78067 and 78071) and from Trout Creek, Alvord drainage, both in Harney County, Oregon, are typical *vagrans* and do not show intergradation with *biscutatus*. Specimens from the Deschutes River are also typical *vagrans* and are separated from *biscutatus* by a barrier of high mountain ranges between the Deschutes and Klamath basins.

A juvenile (Univ. Mich. Mus. Zoöl. No. 78072) from Crump Lake, Lake County, Oregon, has a distinct yellow dorsal stripe, paler than in typical *biscutatus* and with slight brownish suffusion. The dorsolateral area is nearly uniform brown with black spots so reduced in size as to be hardly noticeable. The ventral surface is dusky, finely dotted with black posteriorly. The parietals are reticulated with black, but the top of the head is mainly dull brown in color. The supralabials are pale gray. This specimen is intermediate between *vagrans* and *biscutatus* but is probably nearer the latter.

Geographic variation in distinctness of the dorsal stripe is evident. Specimens from the extreme eastern part of the range in Arizona and New Mexico and those from the arid valleys of the Great Basin, including most of Nevada, Utah, and extreme southern Idaho, and southern Wyoming, have narrow, weakly developed dorsal stripes, which are not distinctly yellow but much suffused with the brownish ground color, and often discontinuous, being interrupted by the upper row of dorsolateral black spots. Most of these specimens also have pale brown ground color. In specimens from the Rocky Mountain region in Colorado, Montana, and central and northern Idaho, the dorsal stripe is usually wider, less suffused with the brownish ground color, more distinctly yellow, and altogether much more conspicuous. This is also true of specimens from Vancouver Island. Along the western edge of its range, *vagrans* shows the same tendencies further developed, and culminating in the color patterns of *biscutatus* and *elegans*. The sporadic occurrence of populations having unusually distinct dorsal yellow stripes and contrasting dark ground color seems to be correlated with existence in mountainous regions under more humid climatic conditions, whereas populations having indistinct stripes and pale ground color in general occur in more arid climates and at lower elevations. In mountainous regions where rainfall is higher, riparian vegetation more extensive, and meadow habitats often available, these snakes are less closely confined to the immediate vicinity of water and often frequent meadowland, brush, and the edges of damp woods. There the distinct stripe contrasting with the dorsal ground color would probably have protective value, since the pattern would conceal the movement of the snake as it crawled beneath thick cover with only part of its body visible. Under such circumstances the section of the snake's body in view seems to shrink and suddenly vanish before the eyes of the observer, who is hardly conscious that it is in motion, because of the longitudinal continuity of color. When this pattern is well developed, there are no transverse markings or color boundaries which, in a moving snake of spotted or checkered pattern, would catch the eye of the observer, and so betray the direction and approximate rate of travel.

In more arid climates snakes would necessarily be more closely confined to the immediate vicinity of water; a brightly colored stripe and contrasting pattern would be disadvantageous, making the snake conspicuous as it lay fully exposed to view on bare rocks at the water's edge or foraged beneath the surface.

Habits and habitat.—Habitat data for *vagrans* include those of Dice (1916: 303–312), Brooking (1934:95), Ruthven and Gaige (1915:11), Cary (1911: 40 and 45), Taylor (1912:355), and the unpublished field notes of C. H. Richardson, D. M. Hatfield, H. G. White, S. B. Benson, and H. S. Fitch. Of 92 snakes for which separate data are available, 8 were found in situations away from the water, 42 were within a few yards of the water or in riparian associations, 42 were actually in the water when seen, or they dove in in an effort to escape. Three authors describe *vagrans* as usually aquatic, whereas a fourth states that it is found mostly in riparian habitats. Apparently *vagrans* is limited to regions with a permanent supply of water, and usually remains near the water's edge in riparian associations. It frequently forages in water, upon which it mainly depends as a retreat from danger. However, it is not necessarily closely restricted to the immediate vicinity of water by ecologic limitations; on occasion, individuals may forage away from the immediate vicinity of streams and even in dry situations.

Ruthven and Gaige (1915:33), Richardson (1915:433), Tanner (1930:43), and Wood (1935:100) have published data on the feeding habits of *vagrans;* the unpublished field notes of W. P. Taylor, J. Dixon, and J. Arnold supply additional data. Most of the feeding data presented below were obtained by making stomach examinations on preserved specimens. To summarize: 69 snakes contained food comprising in the aggregate 172 separate items; 32 snakes had eaten aquatic animals; 37 had eaten animals which are mainly terrestrial and which were probably caught out of the water, but most of them in riparian associations. Fishes were eaten most often; 16 snakes had used this kind of food (*Cottus, Pantosteus, Apocops,* and probably others). Tadpoles had been eaten by 9, slugs by 6, earthworms by 7, mice (*Peromyscus* and *Microtus*) by 6, leeches by 6, lizards (*Sceloporus, Uta, Eumeces*) by 5, toads (*Bufo* and *Scaphiopus*) by 6, frogs by 3, birds (*Passerella*) by 3, salamanders (*Ambystoma* larvae) by 3, tree toads by 1, and snails by 1. Of the individual animals eaten, slugs were most numerous with a total of 33; others, in order of decreasing frequency, were: 30 tadpoles, 23 leeches, 17 fish, 16 snails, 15 earthworms, 9 salamanders, 7 toads, 7 mice, 6 lizards, 4 birds, 3 frogs, 2 tree toads.

Vagrans thus consumes a greater variety of food than any other subspecies of the group, and utilizes, in general, all the food sources used by the other subspecies. Although the specimens represented are from a large area, there is no conclusive evidence of differential feeding habits in different parts of the range. Local seasonal changes in food preferences or availability are not evident.

Generalized feeding habits in *vagrans* may be correlated with the absence of other garter snakes throughout much of its range; it has not been forced into a narrow ecologic niche by the competition of closely related specialized forms. In the arid Great Basin region, garter snakes are necessarily confined to the near vicinity of watercourses, whose small size and isolation, chemical impurity, high temperature, and seasonal volumetric fluctuations result in a scarcity of aquatic life. Here the aquatic ecologic niche alone is not extensive enough to support garter snakes at all seasons, and generalized feeding habits are perhaps necessary in the forms that occur there.

Records of occurrence.—Specimens examined, 514, in the University of Michigan Museum of Zoölogy (unless otherwise indicated), from the following localities:

Alberta: Rocky Mountain Park, 3; Banff, 11.

British Columbia: Stuie, 40 miles east of Bella Coola, 2[1]*; 5 miles south of Buck Island, north of Thompson River, 1[1]; Seton Lake Portage, 1[9]; Nicola Lake, 1[8]; Mission Creek near Kelowna, 1[6]; Departure Bay, 1[9]; Brent's Lake near Summerland, 1[8]; Summerland, 2[8]; Vancouver, 1[8]; Metchosin, 1[9]; "Vancouver Island," 3[8]; no specific locality, 1[9]; Marron Lake, 1[9].

Montana. *Glacier County:* Glacier National Park, 1. *Flathead County:* Big Fork, Flathead Lake, 7; Big Fork, 4. *Yellowstone County:* Billings, 1.

Idaho. *Latah County:* Troy, 1. *Idaho County:* Castle Creek Ranger Station, 1800 feet, south fork of Clearwater River, 1[1]. *Adams County:* ½ mile east of Black Lake, 6800 feet, 3[1]; 1 mile north of Bear Ranger Station, southwest slope of Mount Smith, 5400 feet, 1[1]. *Washington County:* 1 mile northeast of Heath, 2[1]; 1 mile northwest of Heath, Cuddy Mountain, 4000 feet, 1[1]; Crane Creek, 15 miles east of Midvale, 2800 feet, 3[1]. *Fremont County:* Island Park, 3; Snake River near Yellowstone National Park, 7; inlet to Henry's Lake, 1; Sheridan Creek, 1. *Boise County:* Idaho City, 3. *Butte County:* Pass Creek, tributary of Lost River, 1. *Ada County:* Boise, 3; near Boise, 9; six miles west of Boise, 1. *Teton County:* 3 miles southwest of Victor, 6300 feet, 1[1]. *Blaine County:* Petit Lake, 7000 feet, 1[1]; Alturas Lake, 7000 feet, 9[1]; Warm Springs west of Ketchum, 2; Guyer Hot Springs near Ketchum, 1. *Bonneville County:* 7 miles west of Idaho Falls, 1[1]. *Bingham County:* 2 miles southwest of Aberdeen, 1[1]; *Owyhee County:* Homedale, 1[1]; Snake River north of Murphy, 2[4]; Reynolds Creek 12 miles south of Snake River, 2[1]; Castle Creek 8 miles south of Oreana, 1[1]; Indian Creek 2 miles south of Riddle, 7000 feet, 1[1]. *Lincoln County:* Little Wood River, 1[1]. *Cassia County:* Elba, 1[1].

Washington. *Stevens County:* Springdale, 6. *Whatcom County:* Bellingham, 10[1]. *Mason County:* Hoodsport, 2; Lake Cushman, 1. *Whitman County:* Bald Butte, 1[7]; Pullman, 9 (5[7]). *Columbia County:* Humpeg Falls, 1[1]. *Walla Walla County:* Touchet River, 2 miles east of Prescott, 1; Prescott, 4 (1[1]); Wallula, 2[1].

Oregon. *Umatilla County:* Echo, Umatilla River, 1; Pendleton, 18[1]. *Wheeler County:* 17 miles east of Mitchell, 1[1]. *Jefferson County:* Crooked River, 10 miles south of Culver, 4[1]. *Deschutes County:* Cline Falls, 4 miles west of Redmond, Deschutes River, 9[1]. *Harney County:* 6 miles northeast of Fields, 1; Trout Creek, Alvord drainage, 6; Borax Lake, 2.

South Dakota. *Custer County:* Grace Coolidge Creek 3 miles above state game lodge, 4.

Wyoming. *Yellowstone Park:* Swan Lake, 1[1]; no definite locality, 7. *Teton County:* "south of Yellowstone Park," 2; Buffalo Fork of the Snake River 10 miles above Elk, 1. *Natrona County:* Sweetwater River, 1. *Platte County:* 15 miles west of Wheatland, 1[4]. *Sweetwater County:* head of Bitter Creek, 1[1]; Kinney Ranch 23 miles southwest of Bitter Creek, 1[1].

Utah. *Morgan County:* Weber River near Devils Slide, 3[6]. *Summit County:* 22 miles east of Coalville, 1; 8 miles east of Kamas, 2[1]. *Daggett County:* 1. *Uinta County:* 5. *Tooele County:* Grantsville, 1[4]. *Salt Lake County:* Salt Lake Valley between Salt Lake City and Saltair, 5. *Duchesne County:* Little Cottonwood Cañon, 1; Salamander Lake, 1. *Wasatch County:* Creek near Heber, 1; Provo River between Charleston and Midway, 6[6]. *Utah County:* Mount Timpanogos, 6. *Sampete County:* Maple Cañon, 1. *Millard County:* 8 miles northwest of Delta, 2[4]; Oak Creek Cañon, 12 miles east of Delta, 19[4]. *Grand County:* near Moab, 7; Moab, 1. *Beaver County:* Beaver River, 4 miles below Beaver, 1. *San Juan County:* Goodridge 4000 feet, 1. *Kane County:* Caves Lake Cañon 7 miles northwest of Kanab, 3; Cedar Mountain near Kanab, 4.

Nevada. *Elko County:* Goose Creek, 5000 feet, ½ mile west of Utah state line, 3[1]; summit of Jarbidge Mountains between Copper and Coon creeks, 4[1]; Marys River, 22 miles north of Deeth, 5800 feet, 3[1]; Deeth, 1[2]; 3 miles south of Halleck, 2[2]; summit of Secret Pass, 6200 feet, Ruby Mountains, 1[1]; Elko, 1[2]; Jerry Creek, north end of Ruby Lake, 2[1];

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* Explanation of references: [1] Museum of Vertebrate Zoölogy, University of California; [2] United States National Museum; [3] California Academy of Sciences; [4] Collection of L. M. Klauber; [5] San Diego Society of Natural History; [6] Natural History Museum, Stanford University; [7] Charles R. Conner Museum; [8] Royal Ontario Museum; [9] Provincial Museum of British Columbia; [10] University of Nevada Zoölogy Department; [11] Mesa Verde National Park.

south fork of Long Creek, Ruby Mountains, 1^1; Ruby Lake, 1^1; west side of Ruby Lake 3 miles north of Elko County line, 1^1, and 6 miles north of Elko County line, 1^1; Harrison Pass Ranger Station, Green Mountain Cañon, 1^1; Kleckner Creek, Ruby Mountains, 1^1; Willow Creek 2 miles north of White Pine County line, 1^1. *Humboldt County:* Thousand Creek Flat, 2^1; 30 miles southwest of Denio, 1; Virgin Valley, 1^1; Pine Forest Mountains, 6^1; Quinn River Crossing, 4100 feet, 5^1; base of foothills, Black Rock Desert, 2. *Washoe County:* 4 miles southwest of Diessner, 5800 feet, 1^1; Little High Rock Creek, 1^1; Grass Valley Creek, tributary of High Rock Creek, 1; Wall Cañon, 1; Lost Creek, 2; Horse Cañon Spring, 2; Fish Creek, 2; Pyramid Lake, on island, 1^2; "Camp 12, Truckee River," 9^2. *Eureka County:* Maggie Cañon between Seetoya and Cortez ranges, 3. *Lander County:* Battle Mountain 90 miles north of Austin, 1^3; Silver Creek, 1^2; Big Creek, Toyabe Mountains, 7000 feet, 1^1; Kingston Ranger Station, 5^1; Mahogany Cañon, 8000 feet, 1^1; Reese River Valley, 7 miles north of Austin, 3^1. *White Pine County:* Wenzell, 1^1; Willow Creek 2 miles south of county line, 1^1; summit of Overland Pass, 1^1; Piermont, 1^2; Cleveland Ranch, 6100 feet, Spring Valley, 1^1; Snake Valley, 2^3; Baker Creek at 5800 feet, 3^1; 6600 feet, 1^1, 7200 feet, 8^1; Willard Creek, 7150 feet, Spring Valley, 2^1; Spring Valley, 2; White River, 1. *Nye County:* Peavine Creek, 6600 feet, Toyabe Mountains, 1^2; Millett Post Office, 5500 feet, 1^1; 5 miles southeast of Millet Post Office, 2^1; Greenmonster Cañon, 8200 feet, Monitor Mountains, 1^1; 1 mile east of Jefferson, 7600 feet, 1^1; Ash Meadows, 2^3; Ballinger Ranch, Ash Meadows, 1^1. *Mineral County:* 3 miles south of Schurz, 4100 feet, 1^1. *Esmeralda County:* Chiatovitch Creek, 8200 feet, 1^1; Fish Lake, 4800 feet, 5^1. *Lincoln County:* 3½ miles north of Eagle Valley, 5600 feet, 7^1.

Colorado. *Larimer County:* Fort Collins, 1; Estes Park, 1^4. *Routt County:* 4. *Grand County:* 6 miles north of Grandlake, 1. *Boulder County:* Arapahoe Falls, 1; near Pine Cliff, 1. *Jefferson County:* Watertown, 25 miles southwest of Denver, 8^4. *Douglas County:* Sedalia, Devils Head, 1. *El Paso County:* Utes Pass Trail above Long's ranch, 7300 feet, 1^1; Cabin Creek, 9700 feet, east slope of Pikes Peak, 1^1; Minnehaha, 8500 feet, 2^1, and 8300 feet, 1^1; Pikeview Station 2 miles north of Colorado Springs, 6100 feet, 1^1; Hell's Gate, Halfway House, 9000 feet, 1^1; Pikes Peak, 11; Palmer Lake, 1. *Gunnison County:* 2½ miles south of Gothic, 2. *Montrose County:* Paradox, 1. *Fremont County:* 5 miles northeast of Cañon City, 1. *Saguache County:* 3 miles north of Elko, 1. *Huerfano County:* Walsenburg, 4; near Rouse Junction south of Walsenburg, 1; Cuchara Cañon, 9; Spanish Peaks, 8000 feet, 4. *Rio Grande County:* San Luis Valley near Monte Vista, 2. *Montezuma County:* Mesa Verde National Park at Mesa Verde, 1^{11}, Soda Cañon near Far View House, 1^{11}; School Section Cañon, 1^{11}, and north fork of West Mancos River, 10,000 feet, 1^{11}.

California. *Mono County:* Mono Lake Post Office, 6500 feet, 1^1; Walker Lake, 8000 feet, 1^1; Dexter Creek Meadows, 4^5; Hot Creek 2 miles north of Geysers, 1^1; Mammoth, 2^1. *Tulare County:* Quaking Aspen Meadows 3 miles east of Nelson, 3^1; Funston Meadows, 1^1; Trout Creek, 6000 feet, 1^1; Taylor Meadows, 7000 feet, 1^1; Cannell Meadows 6 miles west of Taylor, 7500 feet, 1^1; Emerald Lake, Marble fork of Kaweah River, 1^1. *Inyo County:* Owens Valley 6 miles south of Big Pine, 1.

Oklahoma. *Cimarron County:* ½ mile southeast of state monument, 1.

New Mexico. *Taos* (or *Rio Arriba*) County: Rio Grande between Taos and Espanola, 5. *Rio Arriba County:* 14 miles northwest of El Rito, 1; near El Rito, 3. *More County:* Sapello River at Watrous, 3; *McKinley County:* 5 miles north of Thoreau, 1^1. *San Miguel County:* Pecos, 1. *Lincoln County:* Bonita Cañon, 2. *Grant County:* 5 miles north of Pinos Altos, 2.

Arizona. *Coconino County:* Long Valley, 2^4; 12 miles northeast of Flagstaff, 1^1; 4 miles west of Williams, 1. *Apache County:* north fork of White River, White Mountains, 4^5.

Published records of the occurrence of *vagrans* include: for British Columbia, Sumas Prairie, North Orca Island in the Gulf of Georgia, and Victoria (Boulenger, 1893:203); for Washington, Sheep Creek at Springdale, Stevens County (Blanchard, 1921:5), and Diamond Lake, Stevens County (McLain, 1899:12).

Van Denburgh and Slevin (1918:241) recorded Idaho specimens from Potlatch Creek and Clearwater River near Lewiston, Nez Perce County; Weiser, Washington County; Arco and near the head of Big Wood River, Blaine County; Cottonwood Creek, Cassia County; Payette Lake, Boise County; Fort Hall, Bingham County; Shoshone Falls, Jerome County; and Snake River near Salmon Falls, Twin Falls County.

Tanner (1929:49) recorded Utah specimens from near Mount Myria south of Deep Creek Mountains, Juab County; and (1930:43) from east boundary of Zion National Park. Wood (1935:100) recorded specimens from Vernal, Uinta County.

Yarrow (1875:551) recorded specimens from New Mexico, from Willow Springs, Union County; San Juan River, San Juan County; Taos, and Penasco, Taos County; San Idelfonso, Santa Fe County; Sierra Blanca, Lincoln (or Otero) County.

King (1932:99) recorded specimens from Mormon Mountain, Coconino County, Arizona.

Ortenburger (1927:48) recorded specimens from 4 miles northwest of Kenton, Cimarron County, Oklahoma.

Colorado records include: Wales Cañon, Pueblo County (Boulenger, 1893:203); Meeker, Rio Blanco County (Cary, 1911:27); North Park at Higho and near Pearl, Jackson

County; and Snake River east of Slater, Routt County (Cary, *op. cit.*, pp. 40 and 45). Yarrow (*op. cit.*, p. 552) recorded specimens from Twin Lakes, Lake County; San Luis Valley, Costilla County; Conejos, Conejos County; and Pagosa, Archuleta County. Barry (1932:103) recorded specimens from Baca County.

Thamnophis ordinoides biscutatus (Cope)

(Klamath Garter Snake, Cope Garter Snake)

Eutaenia biscutata Cope, 1883:21 (original description)
Eutaenia brunnea Cope, 1892:654
Eutaenia elegans lineolata Cope, 1892:655 (part)
Thamnophis vagrans biscutata, Van Denburgh, 1897:212 (part)
Eutaenia elegans biscutata, Brown, 1903:291 (part)
Thamnophis ordinoides elegans, Ruthven, 1908:138 (part)
Thamnophis ordinoides biscutatus, Van Denburgh and Slevin, 1918:245 (part)

Type.—Evidently juvenile; collection of E. D. Cope (Cope, 1900:1033, fig. 282), present whereabouts unknown, collected at "shores of Klamath Lake, Oregon" by E. D. Cope.

Range.—Klamath Lakes basin, upper Klamath River, and Warner Lakes basin in south-central Oregon and northeastern California (see fig. 6).

Diagnosis.—Maximum number of scale rows on anterior portion of body 23 or 21, 5th (when 23 are present) of variable length, confined to anterior half of body; 6th extending posteriorly beyond mid-body; 4th extending more than two-thirds the distance to the anus; supralabials 8, 8; infralabials 10, 10; preocular frequently divided by horizontal suture on one or both sides; gastrosteges 184–160 (average for males 173.1, for females 166.1); dorsal stripe yellow and distinct, dorsal ground color dark brown, nearly black, in large part obscuring superimposed black spots; iris dark, heavily pigmented, with narrow, pale, yellowish margin encircling pupil; size large (head and body length of 700 mm. often attained or exceeded); body thick in proportion to length.

Coloration.—Description of freshly killed adult female, Mus. Vert. Zoöl. No. 17352, from the Klamath River two miles below Keno, Klamath County, Oregon.

Supralabials mainly Grayish Olive; anterior ones paler, especially on lower portions, marked with black along their posterior margins; iris appears almost black but has pale, narrow, yellowish, inner rim encircling pupil; dorsal stripe Mustard Yellow, involves middorsal scale row and adjacent half of each scale of rows on either side, faint posteriorly, but continuous to distal portion of tail, involves skin between scales only in neck region; ground color of body Chaetura Black, paling to Olive-Brown on tail; lateral flecks on body Sea-foam Yellow; scales of lateral stripe Deep Olive-Buff, their upper front margins edged with Citron Yellow, or (on posterior part of body) with Barium Yellow; lateral stripe bright and well defined anteriorly, but dull posteriorly, not well defined on tail, where there is gradual transition from dark dorsal ground color to pale color of ventral surface; two rows of black spots in region of lateral stripe, each spot involving base of scale and adjacent skin; inconspicuous unless skin is stretched; chin ivory white; gastrosteges Light Olive-Gray with narrow posterior edges of Tilleul Buff, clouded with suffusion of black pigment which is most pronounced on posterior half of body.

Comparisons.—*T. o. biscutatus* intergrades with the subspecies *elegans*, *vagrans*, and *hydrophila* in different parts of its range. Comparisons with each of these forms is made below.

Differs from *elegans* in its duller dorsal and lateral stripes, as opposed to bright stripes, which lack dusky suffusion in typical *elegans;* in its slightly paler, grayer ground color upon which superimposed black spots are sometimes discernible, as opposed to black or nearly black dorsolateral area of *elegans*, upon which superimposed black spots are usually completely obscured; in its large and often conspicuous greenish or bluish lateral flecks, as opposed to the small paler flecks of *elegans*, which are mainly confined to skin between scales and hence are invisible unless skin is stretched; in the slightly dusky, brownish suffusion on supralabials, especially on their upper portions, whereas supralabials in *elegans* tend to be paler, with little or no brownish suffusion (*biscutatus* is intermediate between *elegans* and *vagrans* in this character, but is nearer to *elegans*); in frequently having brown or gray coloring on top of head on supraoculars, frontal, or parietals, whereas in typical *elegans* top of head is velvety black except in rostral region; in frequently divided preoculars, as opposed to normally undivided preoculars of *elegans;* in frequent possession of maximum of 23 scale rows on body, as opposed to maximum of 21 (occasionally 19) rows in *elegans;* in narrower head and narrower muzzle as opposed to broad head, distinct from neck, with short, blunt muzzle in *elegans;* in larger size (see p. 8); in thicker body.

Differs from *vagrans* in its bright yellow dorsal stripe, which is usually only slightly suffused with dusky coloring, and which contrasts sharply with dark ground color, as opposed to pale yellowish brown or tan dorsal stripe in *vagrans,* often narrow or broken and suffused with dusky pigment, not in sharp contrast with brown ground color; in its dark, nearly black dorsolateral area with obscure black dorsolateral spots, as opposed to brown (frequently pale) dorsolateral area of *vagrans* with its distinct black spots; in its pale supralabials, which contrast with dark ground color of body and bear wedge marks posteriorly, as opposed to duller supralabials of *vagrans,* which approximate shade of brown ground color and often lack wedge marks; in predominantly black color of top of head which extends anteriorly onto frontals and supraoculars, as opposed to predominantly brownish color anterior to parietal plate in *vagrans;* in frequently divided preoculars (see p. 47), as opposed to normally undivided preoculars of *vagrans;* in frequent possession of maximum of 23 scale rows on body, as opposed to maximum of 21 rows (with rare exceptions) in *vagrans;* probably in larger average size.

Differs from *hydrophila* in its well-developed, yellow dorsal stripe, continuous for full length of body, as opposed to dull, faint, narrow, pale brown or tan stripe usually restricted to anterior part of body, sometimes wanting in *hydrophila;* in its distinct, pale lateral stripes, sometimes wanting in *hydrophila,* or, if present, usually suffused with dull color and indistinct; in dark, nearly black ground color of head and body which obscures superimposed dorsolateral black spots, as opposed to gray ground color of *hydrophila,* which is marked with large squarish spots in conspicuous checkered pattern; in its shallower, blunter supralabial wedge marks, as opposed to deeper, slenderer wedge marks of *hydrophila,* which often extend downward to edge of mouth; in its dark iris, heavily clouded with pigment except for pale yellowish inner margin around pupil, as opposed to uniformly pigmented, pale, gray or brown iris of *hydrophila;* in frequently divided preoculars, as opposed to normally undivided preoculars of *hydrophila;* in frequent possession of maximum of 23 scale rows, as opposed to maximum of 21 rows or (more frequently) 19 rows in *hydrophila;* in greater numbers of gastrosteges and urosteges; in large size of posterior supralabials, as opposed to comparatively small posterior supralabials of *hydrophila;* in subequal anterior and posterior genials, as opposed to relatively long posterior genials of *hydrophila;* in larger size; in relatively smaller eye.

Remarks on nomenclature and systematics.—Cope in his original description (1884:21) referred to this form as the most distinct of the genus. His two specimens were both young and he mentioned their small size as a possible diagnostic character, but actually *biscutatus* is a large form. In both of Cope's specimens the "5th" scale row was present, and preoculars were divided. The ventral count of 156 given for the type is well below the minimum (160) in more than 250 specimens examined by me, and is probably erroneous.

Later writers have often synonymized this race. Ruthven (1908:138) was convinced that it was impossible to recognize it as distinct from *"elegans"* (=*vagrans* of present account).

Van Denburgh recognized *biscutatus,* but included under this name, besides the Klamath garter snake, *vagrans* from the Puget Sound region and *hydro-*

phila from the area between the Klamath basin and the Pacific Coast. It is noteworthy that in the scale counts published by Van Denburgh and Slevin (1918) these specimens stand out sharply from the large series from Klamath Falls; most of them do not even overlap the extremes of the large Klamath Falls series with respect to numbers of gastrosteges.

Geographic variation and intergradation.—In the western part of its range in the region of Klamath Lake and the upper Klamath River, *biscutatus* occurs in its most typical form. The measurable characters which set it off from the closely allied races *elegans* and *vagrans* are nowhere constant in all individuals of a geographic population, but merely represent strong tendencies. The majority of specimens from Klamath Falls and the upper Klamath River have 23 scale rows on the body, and nearly half have at least one divided preocular. In those from the eastern portion of the Klamath basin, Sprague River, and Goose Lake the preocular is divided less frequently and the 5th scale row is more often absent, but in coloration and general appearance they seem identical with typical *biscutatus*. Snakes from the Warner Lakes basin east of the Warner Mountains differ sharply in that they have a distinctly brown ground color, in contrast to the nearly black color of typical *biscutatus;* they also differ in scutellation. These specimens are intermediate in appearance between *biscutatus* and *vagrans*. The dorsal black spots are much reduced, so that they are inconspicuous, and the general color is brown. The name *brunnea* (Cope, 1892:654) was based on such specimens. In their robust body form and relatively narrow heads these snakes resemble typical *biscutatus* and differ from *elegans* or *vagrans*. They further differ from *vagrans* in having the ventral surface immaculate or but slightly spotted with black. Specimens from the next hydrographic basin to the eastward, Trout Creek of the Alvord River drainage, are typical of *vagrans* in all respects.

Specimens from the upper course of the Pit River and from Eagle and Grasshopper lakes in Lassen County, California, have been placed with *elegans* but seems to show affinity to *biscutatus*. They differ from typical *elegans* in having the head less distinct from the neck, in often having divided preoculars or a "5th" scale row, in being of large size, and in having a relatively narrow nasorostral contact and relatively long posterior genials. They resemble *biscutatus* in their aquatic habits. On the whole, snakes from the Warner Mountains are so nearly intermediate between the three subspecies *elegans, biscutatus,* and *vagrans* that it is difficult to decide which they resemble most.

There are no barriers to separate *elegans* from *biscutatus* in this region. Numerous small creeks, lakes, and marshes in the Warner Mountains open the way for continuity of garter-snake populations from the Klamath Lake drainage to that of the Pit River.

On the north and west, however, the range of *biscutatus* is sharply circumscribed. The terrain rises abruptly north of Klamath Lake to a high, arid plateau of the Canadian Life Zone with scattered forests of lodgepole and Jeffrey pine, and an absence of watercourses over wide areas. Apparently, no garter snakes of the *Thamnophis ordinoides* group occur in this region. Farther north, where the Deschutes River, flowing in a general northeasterly direction, reaches lower altitudes of the Transition Life Zone, the species reappears, represented by typical *vagrans,* which there shows no indication of intergradation with *biscutatus.* On the west the Klamath basin is separated from the Rogue River basin by the crest of the Cascade Mountains, which apparently forms an effective barrier, since *biscutatus* does not occur in the Rogue River basin and I have not found it at high altitudes in the mountains although I have collected extensively in that area.

On the southwest the gorge of the Klamath River breaks through the Sierra-Cascade mountain chain. *T. o. biscutatus* probably occurs throughout this gorge, but to the westward gradually merges into *hydrophila.* Specimens from the Shasta River and Cottonwood Creek are intermediate in coloration, number of scale rows, preoculars, and length of genials, but on the whole are nearer *hydrophila.*

Specimens collected farther down the Klamath River at Beaver Creek and Horse Creek approach typical *hydrophila* more closely; others from Clear Creek, Dillons Creek, Blue Creek, and Bluff Creek are to me indistinguishable from typical *hydrophila* of the Rogue River basin.

In the Rogue River basin where both *elegans* and *hydrophila* occur, it is the latter which is the ecologic counterpart of *biscutatus,* as shown by feeding data and habitats. The fact that *elegans* occurs on common ground with *hydrophila* while *biscutatus* intergrades with *hydrophila* is in itself sufficient proof of the subspecific distinctness of *biscutatus* from *elegans.*

T. o. elegans also occurs in the Shasta River basin along with *hydrophila–biscutatus* intergrades, and has been collected in the mountains at Hyatt Prairie Dam, on the extreme eastern edge of the Rogue River basin on the divide separating this drainage from that of the Klamath River. There is no apparent barrier except the gradually increasing aridity to prevent *elegans* from extending its range the few miles eastward into territory where typical *biscutatus* occurs. Whether this happens or not, and what the relationships of the two forms may be where perhaps they meet, remains to be seen.

In the Rogue River basin *elegans* shows its subspecific characters strongly developed, but with no indication of intergradation with *biscutatus* such as is shown by series from Lassen and Modoc counties, California; rather it tends to show increasing specialization toward terrestrial habits.

Habits and habitat.—Habitat data are available for 67 individuals of *biscutatus,* most of them from the Klamath River gorge at various points between Keno, Oregon, and the California state line, and also from the Sprague River, and from Deep Creek and Twelve-mile Creek, Lake County, Oregon. All were found near margins of permanent streams or rivers. With few exceptions (8 individuals) these snakes were found within 10 feet of the water and many were in the water. Three were collected along the Sprague River in flat meadowland. All others were taken along boulder-strewn stream edges in canyon bottoms. It was noted that where these canyons opened out into level valleys, and the rocky shore lines gave way to swampy ground or meadowland at the stream edges, *biscutatus* was rare or absent and was replaced by *Thamnophis sirtalis.*

Many of the *biscutatus* collected were found foraging, crawling, or swimming among rocks in swift water at the bottoms of the streams. The majority were found basking on large basalt boulders at the water's edge. When alarmed they would slide from these boulders into the water to conceal themselves in niches and crevices among submerged rocks.

Van Denburgh and Slevin (1918:251) were impressed by the enormous numbers of these snakes along the Klamath River when they collected there in 1909, but they remarked that garter snakes were not especially common there in 1918. At the time of my field work in this general region *T. sirtalis* was more common than *biscutatus;* 16 of the latter represent my maximum day's catch.

The great reduction in the garter-snake population of the region is probably an indirect result of human activity. Damming of the river and resultant frequent and sudden changes in water level may have affected unfavorably the environment of certain aquatic animals upon which the snakes depend for food. Intensive fishing of the river and its tributaries may also have produced unfavorable ecologic changes.

Twenty snakes for which feeding data are recorded had eaten 25 individual animals: 10 *Cottus,* 6 minnows, 4 leeches, 3 lamprey eels, 1 frog (*Rana pretiosa*), and 1 tadpole. Fifteen snakes had eaten fishes (all economically unimportant), 2 had eaten leeches, one had eaten lampreys, one had eaten a tadpole, and one a frog. All this prey, with the possible exception of the frog, must have been found in the water.

T. o. biscutatus does not share its range with other members of the species; wherever it occurs it is the only subspecies of *ordinoides* present. This is owing partly to its limited range, and probably also to the aridity of the region, which does not offer a wide variety of ecologic niches for garter snakes, so that any other forms occurring there would probably be direct competitors. *Thamnophis sirtalis* occurs throughout the area occupied by *biscutatus,* and probably competes with it for food. Available feeding data for *sirtalis* in this region do not clearly indicate differences in food preferences, except that it frequently eats animals caught out of water—birds, mice, and frogs. *T. o. biscutatus* occurs mainly along rocky watercourses, whereas *T. sirtalis* seemingly prefers marsh or meadow habitat, and hence is more common and widely distributed in the Klamath basin.

Records of occurrence.—Specimens examined, 339, in the Museum of Vertebrate Zoölogy, University of California (unless otherwise indicated), from the following localities:

Oregon. *Klamath County:* North fork of Sprague River, 1[2][*]; Sprague River 6 miles east of Beatty, 17; Klamath Lake, 1[1]; Klamath Falls, 206[1]; Keno, 1; Klamath River 2 miles below Keno, 20, 10 miles below Keno, 12, in vicinity of Spencer Creek, 33, and 13 miles up the river (by road) from the California state line, 13; 5 miles east of Merrill, 1. *Lake County:* Bridge Creek, 1[3]; Camass Creek near Plush, 1[1]; Drews Creek, 1[2]; Willow Creek 19 miles east of Lakeview, 1; Lakeview, 2[1]; Dismal Swamp 12 miles east of Pine Creek, 4; Deep Creek 6 miles west of Adel, 11; Twenty-mile Creek just above Warner Lake, 1[2].

California. *Modoc County:* Twelve-mile Creek at Oregon state line, 2; Goose Lake Meadows at Sugar Hill, Davis Creek, 6; Parker Creek, Warner Mountains, 2. *Siskiyou County:* west side of Lower Klamath Lake, 2.

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[*] Explanation of references: [1] California Academy of Sciences; [2] University of Michigan Museum of Zoölogy; [3] Natural History Museum, Stanford University.

Thamnophis ordinoides elegans (Baird and Girard)
(Mountain Garter Snake, Elegant Garter Snake, Boyd Garter Snake)

Eutainia elegans Baird and Girard, 1853:34 (original description)
Tropidonotus tri-vittatus Hallowell, 1854:237
Eutaenia elegans, Yarrow and Henshaw, 1878:1638
Eutaenia elegans lineolata Cope, 1892:655 (part)
Thamnophis infernalis, Stejneger, 1893:210 (part)
Thamnophis elegans, Van Denburgh, 1897:207 (part)
Thamnophis vagrans, McLain, 1899 (part)
Eutaenia elegans elegans, Cope, 1900:1036
Thamnophis ordinoides elegans, Ruthven, 1908:138 (part)

Type.—Adult male (?), U. S. Nat. Mus. No. 882; collected in Eldorado County, California, by C. C. Boyle.

Range.—Southern Oregon between coast ranges and divide of Cascade Mountains, from southern end of Willamette Valley southward; across northern California from the Warner Mountains to western parts of Siskiyou and Trinity counties and eastern Mendocino County; Sacramento Valley, and coast ranges of northern California south to Mount Saint Helena, Napa County; Sierra Nevada (except southeastern part), extending into western edge of Nevada along Smoke Creek and Truckee and Carson rivers; San Bernardino Mountains at high altitudes (see fig. 6, p. 32).

Diagnosis.—Maximum number of scale rows on anterior part of body 21 (occasionally 19, rarely 23), the 5th (when 21 are present) usually not continuous from head back to midbody; supralabials 8, 8; infralabials 10, 10; preoculars undivided; dorsal stripe bright yellow, sharply contrasted with black or nearly black ground color of body; lateral stripe dull yellow, distinct; ventral surface pale, immaculate, or but slightly spotted with black; supralabials pale, sharply contrasted with dark ground color of body; some of posterior supralabials and occasionally anterior ones marked on their upper posterior portions with triangular black wedge marks, which are broad at their bases and not extended downward to edge of mouth; top of head mainly black; iris dark, heavily pigmented, with narrow, pale yellow rim encircling pupil; eye relatively small; muzzle blunt; contact of internasals with rostral much exceeds nasorostral contact on either side.

Coloration.—Description of freshly killed juvenile, Mus. Vert. Zoöl. No. 21626; born in captivity from female collected five miles northeast of Beagle, Jackson County, Oregon.

Top of head black, slightly iridescent, paling to Light Grayish-Olive on anterior portions of internasals and on rostral; parietal spots minute, Primrose Yellow; temporal plates black; lowest postocular and lower portion of middle postocular pale yellow, nearly white; preocular mainly white; loreal black posteriorly, pale anteriorly; nasals and first supralabial partly suffused with dark color; other supralabials pale, nearly white, with triangular black wedge marks along their posterior margins, which are mainly confined to the upper half of each scale and do not extend downward to edge of mouth; pupil large, its diameter exceeding width of iris; iris mainly dark brown, with paler, yellowish inner margin around pupil; dorsal stripe Amber Yellow anteriorly, paling to Straw Yellow posteriorly, continuous nearly to tip of tail but less sharply defined on tail than on body, for most of its length involving middorsal scale row and adjacent half of each scale of rows on either side; broader on neck; lateral stripes Primrose Yellow anteriorly, paler and grayer posteriorly, involving 2d and 3d scale rows; lateral flecks Pale King's Blue; chin white, immaculate; gastrosteges Pale Neutral Gray on their anterior portions, with free edges posteriorly paler—Pallid Neutral Gray,—those on posterior part of body faintly marked with black medially; paired rows of black spots on ventral surface, one pair on each gastrostege near its lateral border, inconspicuous on posterior gastrosteges; 1st scale row on each side marked with gray contrasting with paler color of lateral stripe, bearing a row of black spots, each mainly confined to lower front portion of a single scale; lateral ground color Chaetura Black or Chaetura

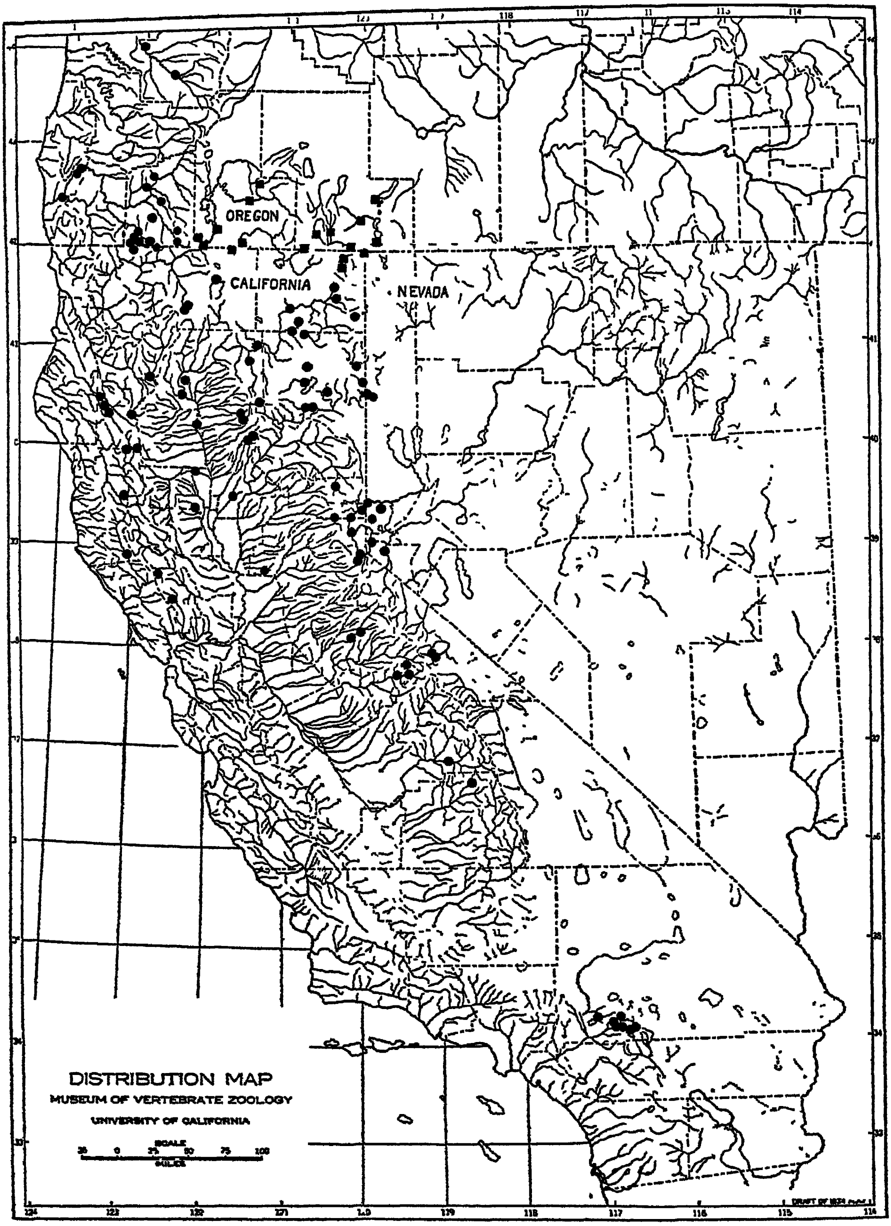

Fig. 6. Ranges, as indicated by specimens examined, of *Thamnophis ordinoides elegans* (dots) in Oregon, Nevada, and California, and of *Thamnophis ordinoides biscutatus* (squares) in southern Oregon and northern California.

Drab obscuring superimposed black spots which are faintly discernible, of rounded outline, and well separated by slightly paler intervening areas.

Comparisons.—*T. o. elegans* intergrades with *biscutatus*, *vagrans*, *hueyi*, and *atratus*, and overlaps in range with *ordinoides*, *hydrophila*, *couchii*, and *hammondii*. Comparisons with *biscutatus*, *hueyi*, *hydrophila*, *couchii*, and *hammondii* are made under the discussions of those forms.

Differs from *vagrans* in color of dorsal stripe, bright yellow rather than pale straw yellow, tan, or dirty white; in black or nearly black, rather than pale brown, ground color, obscuring black dorsolateral spots, which contrast with ground color in *vagrans;* in having top of head mainly black shading into olive in internasal and rostral region, whereas in *vagrans* top of head may be light brown, and black markings are usually confined to parietals and posterior parts of supraoculars and frontal; in pale whitish supralabials which contrast sharply with dark color of body, whereas supralabials in *vagrans* are brown and nearly match brown ground color; in usually well-developed supralabial wedge marks, generally absent in *vagrans;* in lack of black dots on labials, sometimes present in *vagrans;* in immaculateness or light spotting of ventral surface, contrasting with usually conspicuous ventral pigmentation of *vagrans,* which may form extensively continuous black areas; in tendency to loss of "6th" scale row, which is present for most or all of distance from head back to mid-body in *vagrans.*

Differs from *atratus* in lacking bright red markings often present in the latter on dorsolateral area, lateral stripe, and ventral surface; in paleness of supralabials, chin, and ventral surface of body, which are not tinted with bright yellow as these parts often are in *atratus;* in black or dark brown dorsal ground color with no greenish or olive suffusion such as is often present in *atratus;* in possessing distinct lateral stripes, which are sometimes lacking in typical *atratus;* in dark, heavily pigmented iris, as opposed to pale iris of *atratus* (except in northern part of its range); in relatively broader and shorter head, more distinct from neck than in *atratus;* in narrow dorsal stripe as opposed to sometimes broader dorsal stripe of *atratus,* which may include three scale rows for much of its length; in having "6th" scale row of body less reduced than in *atratus;* in having, on the average, more gastrosteges and urosteges.

Differs from *ordinoides* in lacking red coloring often present in dorsal stripe, on sides, or on ventral surface in *ordinoides;* in having bright yellow and well-defined dorsal stripe and well-developed lateral stripes, whereas in *ordinoides* lateral stripe may be obscure or absent and dorsal stripe is sometimes reduced; in black or blackish brown ground color, as opposed to sometimes light brown or chestnut ground color of *ordinoides;* in having supralabial wedge marks, which ordinarily are not developed in *ordinoides;* in wider head much exceeding diameter of neck, as opposed to narrow head, which is not distinct from neck, in *ordinoides;* in nearly always having 21 scale rows as opposed to 19 or usually 17 rows, 8 rather than 7 pairs of supralabials, and 10 rather than 8 or 9 pairs of infralabials; in undivided rather than frequently divided preoculars on each side; in having more than 158 gastrosteges, whereas *ordinoides* generally has fewer than 158; in having, on the average, more urosteges (though with slight overlap in numbers between females of *elegans* and males of *ordinoides*).

Remarks on nomenclature and systematics.—The original description of this subspecies was based on two specimens. Stejneger (1893:211) and Cope (1900:1036), with additional specimens, recognized it as a distinct form. However, Ruthven (1908:138) included *vagrans* as well as the present form under the name *elegans.* He remarked (1908:145): "In the Sierra–Cascade range the color [of his composite race *elegans*] tends to become generally darker, although the pattern of eastern specimens is retained." He pointed out also (1908:143) that specimens from the Sierra Nevada tended to have the number of scale rows on the body reduced, as compared with those from more eastern localities, and interpreted this as showing intergradation with "*ordinoides*" (=*atratus*). He found all intermediate stages in distinctness of dorsal stripe. He regarded this as individual variation and therefore decided (1908:145) that *couchii* should not be distinguished from *elegans.* Also, he expressed uncertainty regarding the relationship of *elegans* to *hammondii,* but implied that these forms might intergrade geographically. Although Ruthven listed Kern Lake as a record station of occurrence for both *elegans* and *hammondii,* he did not comment on this apparent occurrence of the two kinds at the same place.

Van Denburgh and Slevin (1918:235–240) demonstrated the distinctness

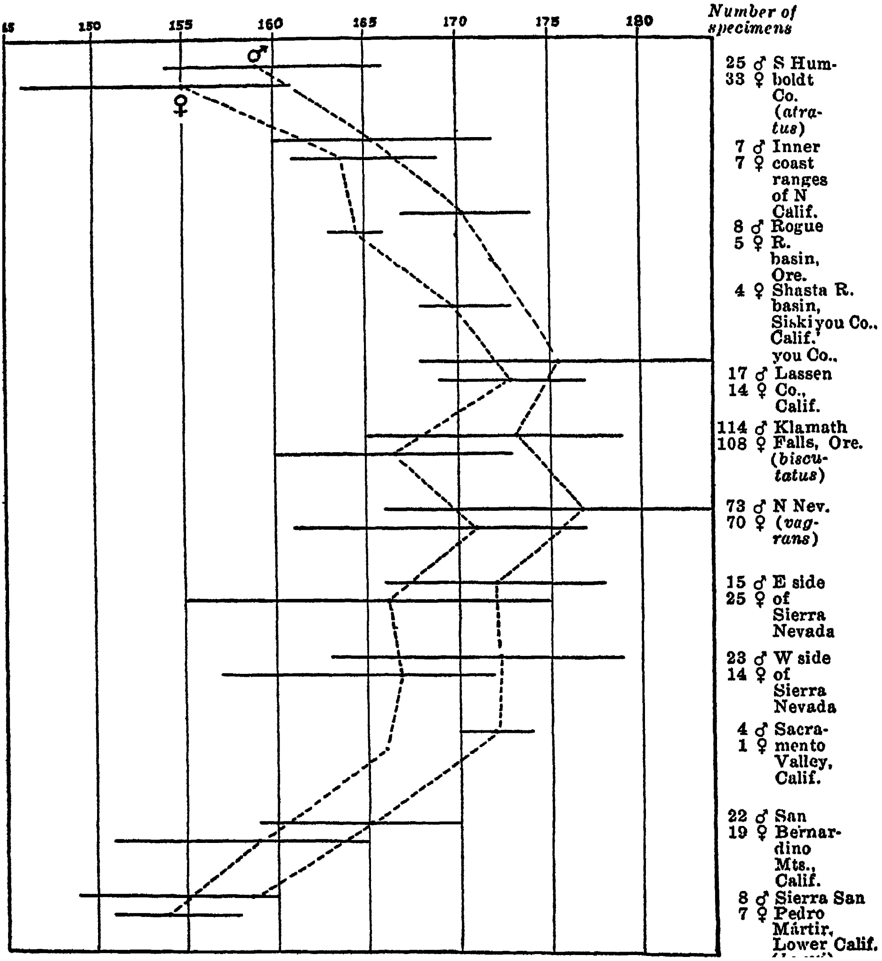

Fig. 7. Numbers of gastrosteges in populations of *Thamnophis ordinoides elegans* and intergrading populations of other subspecies. Note that in Lassen County *elegans* has more gastrosteges than in other parts of its range, thus resembling *biscutatus* and *vagrans,* with which it intergrades; but that in the northwestern and southern parts of its range it undergoes marked reduction in numbers of gastrosteges, showing intergradation with *atratus* and *hueyi,* respectively. Geographic groups are of the subspecies *elegans* unless otherwise indicated.

of *elegans* from *atratus, couchii,* and *vagrans,* and defined its geographic range approximately. However, they failed to show its true relationship to the other subspecies. They classified *elegans* as a subspecies of *ordinoides* on the assumption that it intergraded with *atratus,* but two of the specimens which they regarded as intergrades, from near Siskiyou, Jackson County, Oregon, actually belong to the subspecies *hydrophila.* The other two, from Anderson, Shasta County, California, are typical *elegans. T. o. atratus* is found to be restricted to the coastal region and does not occur within seventy miles of that locality. Nevertheless, intergradation between *atratus* and *elegans* occurs, as shown by specimens from the region immediately west of South Fork Mountain, eastern Humboldt County, California. As shown under my discussion of *couchii,* Van Denburgh and Slevin (*loc. cit.*) erroneously concluded that *couchii* and *elegans* intergrade. The same authors demonstrated that overlapping occurs between *elegans* and *hammondii* in southern California.

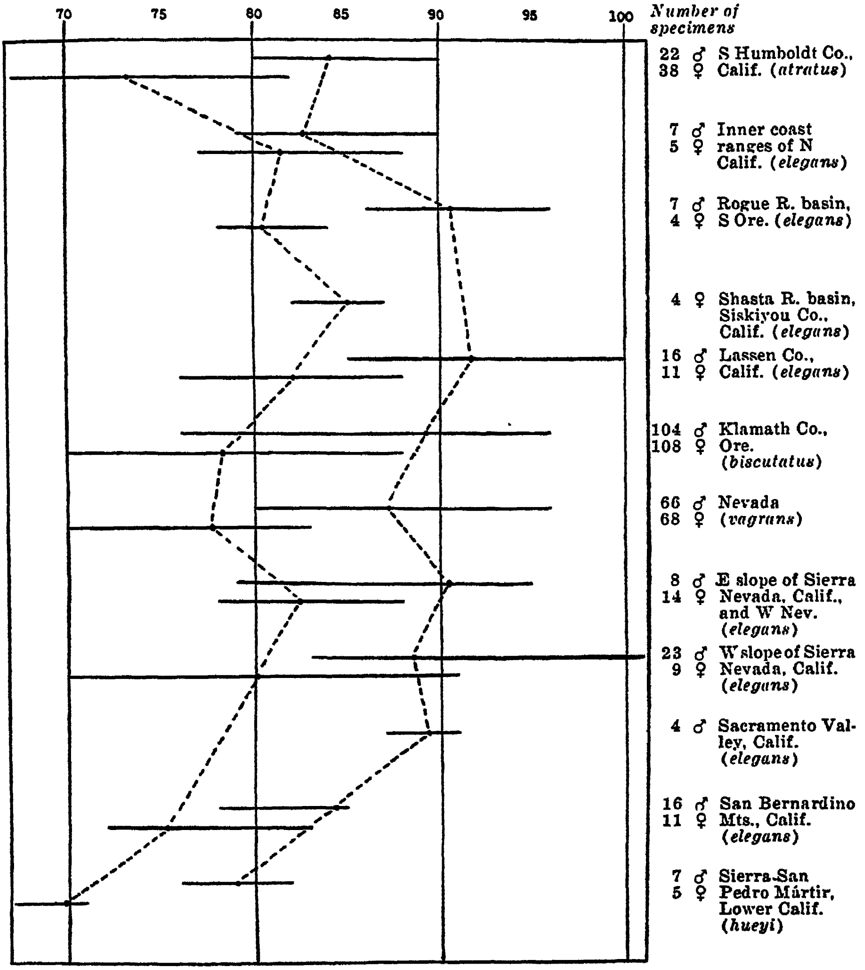

Fig. 8. Numbers of urosteges in populations of *Thamnophis ordinoides elegans* and other subspecies which intergrade with it. Note the high number of urosteges in *elegans* as compared with numbers in other forms, marked reduction in northwest coastal region where intergradation with *atratus* occurs, and even more marked reduction in populations at southern end of range (San Bernardino Mountains), which show an intermediate stage between typical *elegans* and *T. o. hueyi.*

Geographic variation and intergradation.—In Lassen and Modoc counties, California, *elegans* bears resemblances to *biscutatus* that are not found in other parts of its range. In this region it attains large maximum size and most of the adults approach the average size of typical *biscutatus;* elsewhere it is so much smaller that there is little overlapping with *biscutatus* in adult size. Further likeness to *biscutatus* is found in the dark brown, rather than black, ground color, and in the slightly dusky suffusion of the dorsal stripe. In this part of its range *elegans* attains a maximum number of ventrals and subcaudals, and these scales show progressive decrease in numbers to the north, west, and south. This character also links it with *biscutatus.* In relative lengths of scale rows *elegans* from northeastern California agrees closely with *biscutatus,* except in lacking the "5th" row, a vestige of which usually persists in *biscutatus* (making a total of 23); the "6th" row is usually continuous from behind the head posteriorly to a point more than half the distance to the anus, and the "4th" row averages nearly as long as in *biscutatus,* and longer than in *elegans* from most other parts of the range. The body proportions resemble those of *biscutatus,* being more robust than in typical *elegans;* the head is not markedly widened posteriorly nor sharply set off from the neck region. The posterior genials are relatively long as compared with those of *elegans* from other localities, and in this fact is found another point of resemblance to *biscutatus.* As compared with that of northwestern populations of *elegans,* the muzzle is less blunt and the internasorostral contact less markedly exceeds the nasorostral contact on either side, thus showing an intermediate stage toward *biscutatus* (see p. 117).

In the Rogue River basin, Oregon, *elegans* has its subspecific characters strongly developed. The dorsal stripe is bright lemon yellow with no dusky suffusion, the ground color of the dorsolateral area is jet black, and the top of the head is black in the region of the parietals, supraoculars, frontal, and prefrontals, shading into pale brown on the internasals and paler yellowish brown on the rostral. The head is short and broad in appearance, with a blunt muzzle, and the internasorostral contact greatly exceeds the nasorostral contact on either side (average, 135 per cent). In this part of its range *elegans* does not show the reduction in length of scale rows which it does farther south. In one of the specimens examined (Mus. Vert. Zoöl. No. 16337) the "5th" scale row is present for a short distance on the anterior part of the body (making a total of 23); in all other specimens it is absent. The "6th" row is not noticeably reduced and usually extends posteriorly beyond mid-body, averaging more than 50 per cent of the head and body length, though in nearly all it is missing for the length of a few scales in the neck region, thus showing an incipient stage in reduction. The "4th" row also is relatively long, closely approximating that of *biscutatus. T. o. elegans* in this part of its range is slender bodied in appearance and differs in this respect from the population of northeastern California and from the race *biscutatus.* Two specimens from west-central Oregon (Eugene, and middle fork of the Willamette River) agree essentially with those of the Rogue River basin except in having the gastrosteges spotted medially with black. Others, from Siskiyou, Shasta, and Tehama counties, California, are similar in general appearance and in scalation.

Specimens in northern California from as far eastward as the Warner Mountains, Eagle Lake, and Box Springs are definitely nearer *elegans* than *vagrans*, although those from the Warner Mountains region tend strongly toward *vagrans* in characters. The series from Smoke Creek in the vicinity of the California-Nevada state line are intermediate in all respects, but on the whole they seem to be slightly nearer to *elegans*. The ground color is of a dark brown, intermediate shade with distinct superimposed black spots. The dorsal stripe is brighter yellow than in any series of *vagrans* but is much more suffused with dusky coloring than in any other series of *elegans*. They show affinity to *vagrans* in having black blotches ventrally, though these are less extensive than they usually are in *vagrans*. The majority of these snakes have divided preoculars, thus differing from both typical *elegans* and typical *vagrans*, and possibly showing relationship to *biscutatus,* though the percentage of divided preoculars is even higher than in typical *biscutatus* from the Klamath Lake region. They differ from *elegans* in being relatively thick bodied and thus approach *vagrans* or perhaps *biscutatus*. This series of intergrades is as homogeneous in characters as are series of typical *elegans* and typical *vagrans*.

Specimens from southern Washoe County and Douglas County, Nevada, show little evidence of intergradation with *vagrans*. Their heads are mainly dark brown on top with but little black pigmentation except on the parietals; otherwise they are typical of *elegans* in coloration, having bright lemon yellow or orange yellow dorsal stripes, black ground color, ventral surface pale and nearly or quite immaculate. These specimens appear more robust than those from most parts of the range and this character may indicate affinity to *vagrans*. Others from northern and eastern Washoe County also show intergradation, but are nearer *vagrans* and have been discussed under that form.

No specimens are available from the lowlands of west-central Nevada in Churchill and Lyon counties, and it seems probable that in this unfavorably arid region a gap exists between the ranges of the two forms. Farther south, in Esmeralda and Mineral counties, where the terrain is more mountainous and less arid, *vagrans* extends its range farther westward and meets *elegans* in the Mono Lake region. Certain specimens from there are nearly typical of *elegans,* others are nearly typical of *vagrans,* and the majority are in varying degrees intermediate between the two. Intergradation is more irregular in this region than farther north. This fact may indicate that the two forms have here been separated at some time in the past and subsequently brought together again through reinvasion of the area.

South of Mono Lake, *vagrans* extends westward into the high Sierra Nevada and replaces *elegans* at higher elevations.

A single specimen from Owens Valley near Big Pine, Inyo County, California, is possibly nearer *vagrans* but is intermediate toward *elegans*. Its ground color is dark brown and the top of its head is dark brown except for the parietal plates, which are marbled with black. Both supralabials and infralabials are brownish in color. The gastrosteges are dusky and spotted with black. The dorsal stripe is distinctly yellow but slightly suffused with brownish color and is narrow, with irregular edges.

A series from Kings River Canyon, 5000 feet altitude, Fresno County, California (Mus. Vert. Zoöl. Nos. 6266–6275), shows peculiar development of the facial markings. The loreal plate is mainly black except for its upper anterior portion, and this black is continuous with the wedge marks of the 2d and 3d supralabials. Supralabial wedge marks are well developed but more slender and elongate than in typical *elegans;* some extend downward to the edge of the mouth. Black on top of the head is less extensive anteriorly than in typical specimens; most of the frontal and the anterior portion of the supraoculars as well as the prefrontals, internasals, and rostral are brown. In most of these specimens brown is present on the parietals and is reticulated with black. The dorsal ground color of the body is dark brown rather than black. Van Denburgh (1922:828) regarded this series as showing intergradation between *elegans* and *couchii.* Actually none of them shows well-defined tendencies toward *couchii,* a typical individual of which (Mus. Vert. Zoöl. No. 6265) has been collected at Hume only a few miles away. Rather, they merely represent a slightly differentiated geographic population of *elegans,* probably tending toward *vagrans,* which occurs at higher altitudes in the southern Sierra Nevada.

Throughout the Sierra Nevada *elegans* shows a strong tendency toward suppression of the "6th" scale row. In 15 of the 78 specimens examined from this region, this row was absent; in most of the others it showed various stages of reduction. The "4th" row is correspondingly short as compared with that of other populations. The internasorostral contact is relatively narrower than in series from the northwestern part of the range, and almost as narrow as in series from Lassen and Modoc counties. As compared with the latter series, however, the Sierra Nevada snakes show a marked reduction in numbers of gastrosteges and urosteges, as well as in length of scale rows.

Six specimens examined from the Sacramento Valley seem to show no points of difference from those of the Sierra Nevada. Eleven from Trinity County, California, show no apparent differences from typical *elegans* in coloration and general appearance, but the counts of gastrosteges and urosteges are much lower than in any other population except that of the San Bernardino Mountain region. This series also shows the greatest reduction of dorsal scale rows of any of the lots of *elegans* examined; in the four males the "6th" row averages less than 10 per cent of the head and body length, and less than 30 per cent cent in the eight females. The "4th" row is correspondingly reduced (see p. 46). All departures from the characters of typical *elegans* shown by this population are in the direction of the subspecies *atratus;* this population is geographically near to *atratus,* and no marked ecologic differences separate the two forms. Therefore, because their habitats are continuous in that region, it seems apparent that complete intergradation takes place. Specimens taken a few miles farther west in the drainage basin of the Van Duzen River are of similar appearance and scalation, but have a few small red dots on the ventral surface and on the dorsolateral area. As red markings are characteristic of *atratus* but are not found in *elegans,* these specimens have been placed with *atratus.*

In the Sierra Nevada the southernmost locality records for *elegans* are in the Mount Whitney region—Jackass Meadows, Monache Meadows, and Onion Valley—and the subspecies has not been recorded from Kern or Los Angeles counties. All records from the San Bernardino Mountain region were made at high altitudes. A gap of more than 100 miles exists between the known ranges of the population in the Sierra Nevada and that in the San Bernardino Mountains. Future collecting may partly bridge this gap, but probably *elegans* does not occur at present in the extreme southern part of the Sierra Nevada nor in the Tehachapi Mountain region. These low mountains represent an arid phase of the Upper Sonoran Life Zone, where streams are few and mostly intermittent. The parts of the southern Sierra Nevada and the San Bernardino Mountains where *elegans* occurs are higher both zonally and altitudinally and are characterized by a moister climate. Evidently the San Bernardino Mountain population of *elegans* is now widely separated geographically from the northern population, which ranges continuously from Tulare County north into Oregon. As might be expected, this isolated southern population has developed certain well-marked characters. The posterior genials are shortened so that they are actually shorter on the average than the anterior pair, whereas in other series the anterior genials do not average more than 91 per cent of the length of the posterior ones. The internasorostral contact averages relatively narrower than in any other population except those which show intergradation with *biscutatus* and *atratus,* but approximates that of *hueyi.* These snakes have a slightly paler ground color than does "typical" *elegans;* they tend toward dark gray-brown rather than black, and show superimposed black spots, especially in the young. Apparently this population consists of individuals of small size. The one gravid female (Mus. Vert. Zoöl. No. 711) among the specimens examined was smaller than any from other localities, having a head and body length of only 415 mm. Likewise, the five adult males with knobbed keels on scales of the anal region are the smallest specimens of *elegans* in which this secondary sexual character is well developed. This small size is probably a genetic character and may represent the dwarfing effect of an environment which has become progressively more restricted and less favorable, at the periphery of the subspecific range. Small size is not here accompanied by marked reduction in length of scale rows. The "6th" scale row was present in all specimens examined, and in most was continued posteriorly beyond mid-body although with a short gap in the neck region. In this respect the San Bernardino population differs from *elegans* in the Sierra Nevada, where the "6th" scale row is usually reduced and sometimes absent.

Habits and habitat.—To summarize the available habitat data for *elegans:* Of 106 snakes only 7 were found in the water, 67 were found in riparian associations, and 22 in dry situations away from the water. Many of those found in riparian associations or in the water were in localities where streams are partly or wholly dry at some times of year, indicating that a permanent water supply is not an ecologic necessity to *elegans.*

Forty-eight of the specimens examined, representing 33 widely scattered localities, contained food items. The 100 individual animals eaten included 12 fish, 9 leeches, and one tadpole. The remaining 78 were terrestrial, and comprised, in order of decreasing frequency, slugs 30, toads 17, tree toads 9, fence lizards (*Sceloporus occidentalis* and *S. graciosus*) 9, frogs (*Rana boylii* and *R. pipiens*) 5, mice (*Peromyscus* and *Microtus*) 3, earthworms 3, salamanders (*Ensatina*) 1, shrews 1. With the exception of one specimen from Oroville, California, all those snakes (10) which had eaten aquatic animals (fish or leeches) came from a restricted part of the range in Modoc and Lassen counties, California, and from extreme western Washoe County, Nevada. These data corroborate field observations on *elegans* in the same region in indicating differential feeding habits in different parts of the range.

Although slugs exceed all other animals in number of individuals eaten, they are an insignificant proportion of the total volume of food consumed. All the *elegans* found to contain slugs were young or half-grown individuals, most of which were found at the edges of creeks or in damp meadows.

These data seem to justify the conclusion that *elegans* is not dependent on aquatic life for food, but finds nearly all its food on land, and even in dry situations away from water.

Habitat data show that *elegans* has been found most often in riparian associations among bushes or in damp meadows, and that it is seldom found in the water; frequently it occurs in dry situations far from a permanent water supply. Like other garter snakes, *elegans* displays an instinctive tendency to seek out the near vicinity of water, and in this respect differs from snakes of some other genera, which occur typically in dry land habitats in the same region. However, it is not strictly aquatic and does not depend directly on the presence of water either as a source of food or as a place of escape. In this respect *elegans* contrasts sharply with some other forms of *Thamnophis*.

In the course of my field work nearly all the *elegans* encountered away from water were found accidentally; most of them were picked up from roads, although no specimens of the Hydrophila group of subspecies were found in this way, even in regions where they were known to be common. Most of the time given to actual search for garter snakes was spent in following the edges of running streams; a large proportion of the *elegans* found were therefore taken in such situations, though they may have been almost equally abundant elsewhere, where no search was made. The seeming relative scarcity of *elegans* in most localities where it occurs may be due to the fact that individuals are widely scattered instead of being concentrated, as are individuals of some other forms, along the permanent streams.

With few exceptions, the young found were in the immediate vicinity of streams. They were feeding on terrestrial animals characteristic of damp streamside habitat—slugs, earthworms, and recently metamorphosed amphibians. Apparently the young have a stronger predilection for the riparian association than the adults have; small animals suitable for their food are usually more abundant in such moist situations; also, this preference may indicate partial retention of more aquatic ancestral habits.

Adults have been found more often in dry forests at distances from water.

Relatively large animals eaten by them which might have been caught in such dry situations—lizards, mice, toads, and adult tree toads—constituted all but an insignificant portion of the total bulk of recorded food, though comprising less than half the total number of individual animals consumed.

T. o. elegans in Modoc and Lassen counties seems to differ from the subspecies elsewhere in both habitat and feeding habits. My own observations on garter snakes in that region were made mainly at Ash Creek in the extreme northwestern part of Lassen County, and I was impressed by their different behavior and apparently different ecologic situation. *T. o. elegans* was abundant along the creek at the time of my visit; in an afternoon and morning spent hunting them, 25 were seen, whereas 4 represent my maximum day's record of this subspecies at other localities. All were found within 5 feet of the water's edge. One escaped by crawling under a boulder; others made for the water when opportunity offered. Usually they did not dive, but swam across the stream. At Rush Creek, a few miles from this locality, several snakes were seen under similar conditions. Specimens taken by various collectors at Eagle Lake and Grasshopper Lake and on the headwaters of the Pit River presumably were found concentrated in the vicinity of water, since each series was taken within one or two days' time, and the snakes containing food had eaten aquatic animals, either fishes or leeches.

All this evidence seems to show that in Modoc County and northern Lassen County *elegans* is more aquatic than in other parts of its range. This region of differentiation is characterized by a much more arid climate than the rest of its geographic range, being situated on the eastern or Great Basin side of the Sierra-Cascade divide. Except near streams, this region is mainly desert or semidesert, dominated by juniper or sage, or by sparse open forests of yellow pine. In such an environment small animal life is scarce, and daytime summer temperatures are high. It might be expected, therefore, that garter snakes would tend to remain close to water, where animal life is more common and the more abundant vegetation gives protection from high temperatures, these snakes being strictly diurnal.

A biotic factor appears even more important than this physical factor in explaining these observed changes in habits: *Throughout the entire range of elegans this is the only region where no garter snake of the Hydrophila group (hydrophila, couchii, gigas, hammondii, and digueti) occurs.* As will be shown, all members of the Hydrophila group are specialized for aquatic life; they depend on the water as a source of food and as a place of escape from enemies. Where conditions are favorable for them these snakes may be extremely abundant, but *elegans* is less specialized for aquatic life. Probably it tends to be crowded out of the aquatic ecologic niche occupied by the Hydrophila group, and in avoiding competition has broadened and specialized its range of feeding to include mainly terrestrial forms. In the northeastern part of its range no such competition exists, and *elegans* there retains more aquatic habits, which are probably primitive, tending in this respect, as it does in structural characters, toward the geographically adjacent race *biscutatus*, which likewise does not share its range with members of the Hydrophila group.

Although *elegans* and *couchii* occur together throughout the lower part of the Sierra Nevada, *elegans* also occurs extensively at higher elevations above the altitudinal range of *couchii;* hence the name "Mountain Garter Snake." This difference in altitudinal range is undoubtedly correlated with differing ecologic preferences in the two forms, though not necessarily with physiological differences in ability to resist high or low temperatures. The terrestrial habits of *elegans* allow it to take advantage of rising air temperatures and thus to begin foraging as soon as its body temperature is high enough to allow of free motion. Water temperatures at high altitudes ordinarily are low, even in warm summer weather, and streams may be only a few degrees above freezing. Such conditions would be unfavorable to an aquatic snake, since it would be chilled by the low water temperature and would be unable to function efficiently in capturing its food or escaping enemies. Accordingly, *couchii* is restricted to lower altitudes.

The subspecies *elegans* is most characteristic of the Transition Life Zone, but also occurs throughout the Upper Sonoran and in the Canadian life zones. It has been found most often in the vicinity of streams in open woods of yellow pine or oak associations, but occurs under varied climatic conditions and in widely different plant associations. Thus it has been found along streams in the coastal region of southern Oregon and of northern California in the vicinity of dense forests, and in the arid Great Basin regions of Modoc, Lassen, and Mono counties in California. The riparian association which it inhabits probably is less variable in different climates than are either terrestrial or truly aquatic habitats, so that it occurs in both humid and arid regions, in high mountains and in lowlands.

Records of occurrence.—Specimens examined, 253, in the Museum of Vertebrate Zoölogy (unless otherwise indicated), from the following localities:

Oregon. *Lane County:* middle fork of Willamette River at Rolling Riffle Creek, 1; Eugene, 1. *Jackson County:* 5 miles northeast of Beagle, 9; Trail Creek 6 miles above its mouth, 1; Griffen Creek, 1; Hyatt Prairie Dam, 1; Emigrant Creek at Buckhorn Lodge, 1; Antelope Creek, 1; Bear Gulch, Little Applegate River, 1; junction of Big and Little Applegate rivers, 1; mouth of Beaver Creek, Big Applegate River, 1; ridge 2 miles east of Squaw Lake, 1; Cottonwood Creek near Cole in Klamath River drainage, 1. *Curry County:* Rogue River at Solitude Bar, 2, mouth of Burns Creek, 1, and 2 miles west of Agness, 1.

Nevada. *Washoe County:* Tahoe Meadows, Galena Creek, 8500 feet, 1; Smoke Creek 9 miles east of state line, 3, and near state line on south fork (Rush Creek), 11; 8 miles southeast of Reno, 4; Truckee River at Verdi, 1. *Douglas County:* Carson River at Minden, 3; Glenbrook, 3[2][*]. *Washoe, Ormsby,* or *Douglas* counties: "Lake Tahoe," 1[1].

California. *Modoc County:* 5 miles northeast of Eagle Peak, 7000 feet, 1; north fork Pit River, 3[4]; Pit River at Canby Bridge, 1, Rush Creek, 3 (1[4]), and Adin, 1. *Siskiyou County:* Big Applegate River 3 miles south of Oregon state line, 1; Butte Creek 5 miles south of Mount Hebron, 2; 3 miles northeast of Weed, 1; ½ mile south of Weed, 1. *Trinity County:* Grass Valley Creek, 2000 feet, 1; Mad River Camp Ground, 1; Mad River, 2550–3000 feet, 5; divide 12 miles north of Yolla Bolly Mountain, 4400 feet, 2; 6 miles west of South Yolla Bolly Mountain, 5500 feet, 1. *Shasta County:* Pit River near McArthur, 1; Hat Creek 7 miles north of Hat Creek Post Office, 1; Salt Creek 7 miles north of Redding, 1; Anderson, 1[3]. *Lassen County:* Ash Creek 5 miles southeast of Adin, 21; Smoke Creek at Nevada state line, 3; Grasshopper Lake, 15[2]; Petes Valley, 4500 feet, 1; Eagle Lake, 8 (5[2]); 7 miles north of Observation Peak, 1; Drakesbad, Mount Lassen, 1; Susan River 8 miles west of Susanville, 3; 5 miles west of Susanville, 1. *Plumas County:* Willow Lake, 1. *Tehama County:* Lymans, 3300 feet, 4 miles northwest of Lyonsville, 2; Lyonsville Post Office, 3500 feet, 1; Old Lyonsville, 3500 feet, 1; 1 mile northeast of Red Bluff, 300 feet, 1. *Butte County:* Butte

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[*] Explanation of references: [1] United States National Museum; [2] California Academy of Sciences; [3] Natural History Museum, Stanford University; [4] University of Michigan Museum of Zoölogy; [5] Sacramento Junior College Department of Zoölogy.

Creek Meadows, 1; Jonesville, 1; Oroville, 3. *Mendocino County:* Line Creek, 6000 feet, ½ mile east of Castle Peak, 1; Mount Sanhedrin, 1^2; Pieta, 1^3. *Glenn County:* Stony Creek near Orland, 1^2; 3 miles east of Norman, 1. *Sierra County:* Little Truckee River, Sierraville, 1^3. *Lake County:* Middleton, 1^3. *Nevada County:* Truckee, 1^4; Floriston, 3. *Placer County:* Truckee River 2 miles west of Lake Tahoe, 2^1; Soda Springs Station, 1; 5 miles north of Roseville, 1; "near Roseville," 1^5. *Eldorado County:* Fyffe, 1^3; Tallac, 18^3; Fallen Leaf Lake, 4 (1^3, 3^2). *Napa County:* Saint Helena, 1^2. *Mono County:* Farrington's, Mono Lake, 4; 6 miles south of Leevining, 3. *Tuolumne County:* Pinecrest, 1; Glen Aulin, 1; Tuolumne Meadows, 8600 feet, 6 (1^3); 10 miles southeast of Strawberry, 1. *Mariposa County:* Feliciana Mountain, 1; Tenaya Lake Meadows, 5^4; Tamarack Flat, 1^3; Yosemite Valley, 11 (1^3). *Fresno County:* Kings River Canyon, 5000 feet, 10. *Inyo County:* Onion Valley, 1. *Tulare County:* Jackass Meadows, 3; Monache Meadows, 1. *Los Angeles County:* Santa Ana Cañon, 5500 to 6200 feet, 6; Fish Creek, 6500 feet, 3; Cienega, south side of Sugarloaf, 1. *San Bernardino County:* Bluff Lake, 5; Seven Oaks, 5000 to 5100 feet, 2; west fork of Deep Creek, 1^3; Bear Lake, 6700 feet, 1.

Thamnophis ordinoides hueyi Van Denburgh and Slevin

(Huey Garter Snake, San Pedro Mártir Garter Snake)

Thamnophis hammondii, Van Denburgh, 1896:1007

Thamnophis ordinoides vagrans, Van Denburgh and Slevin, 1918:240

Thamnophis ordinoides hueyi Van Denburgh and Slevin, 1923:2 (original description)

Type.—Adult female, Calif. Acad. Sci. No. 56855, collected near Arroyo Encantada, between La Grulla and La Encantada, Sierra San Pedro Mártir, Lower California, Mexico, June 13, 1923, by J. R. Slevin.

Range.—Sierra San Pedro Mártir of northern Lower California, Mexico; evidently confined to high altitudes in Transition Life Zone; known only from vicinity of La Grulla and La Encantada.

Diagnosis.—Maximum number of scale rows on body 21, 5th extending from head posteriorly to mid-body but often discontinuous for short distance on neck, fourth extending posteriorly less than two-thirds of distance to anus; supralabials 8, 8 (sometimes reduced to 7 on one or both sides); infralabials 10, 10 (sometimes reduced to 9 on one or both sides); gastrosteges 149–161; urosteges 67–82; preoculars undivided; ground color dark gray or dark olive; dorsal stripe bright yellow; ventral surface immaculate or but slightly spotted with black; supralabials pale, contrasting with dark coloration of dorsal surface; triangular black wedge marks on upper posterior portions of supralabials, not extending downward to edge of mouth; top of head mainly dark gray; muzzle blunt; combined contact of internasals with rostral much exceeds nasorostral contact on either side; eye relatively small.

Coloration.—Description of Calif. Acad. Sci. No. 56853 adult female (alcoholic).

Top of head Buffy Brown posteriorly, paler anteriorly, near Dark Olive-Buff on prefrontals; irregularly scattered deep marks of black pigment along posterior edges of frontal, and continuously back along suture between parietals; supralabials Massicot Yellow, their upper portions shaded by deep pigment granules; distinct wedge marks on 2d, 3d, 4th, 5th, and 6th supralabials on each side, none reaching edge of mouth; wedge mark on 6th supralabial lacks usual taper, being wider below than above; all are of irregular outline on their anterior borders; an irregular dark mark between temporals and supralabials, on adjacent edges of these scales, mainly confined to temporals; two lower postoculars, nasals, and loreal mainly of same pale color as supralabials, but more or less suffused with dusky pigmentation; lower posterior portion of loreal black; dorsolateral area of body dark brown (between Olive-Brown and Buffy Brown); dorsal stripe Barium Yellow, only a single scale row in width, though adjacent edges of scales lateral to it are yellowish brown, markedly paler than general coloration of dorsolateral area; lateral stripe confined to 2d and 3d scale rows, Marguerite Yellow; parietal spots small, indistinct, their borders not well defined; ventral surface nearly immaculate, Ivory Yellow anteriorly, gradually darkening to Yellowish Glaucous posteriorly; scales of lowest row match ventral surface in coloration.

Comparisons.—*T. o. hueyi* shows intergradation (through overlapping characters) with *T. o. elegans,* and is closely related to *T. o. vagrans,* with which it was formerly included by

Van Denburgh and Slevin (1918:244). Its geographic range is entirely within the range of *T. hammondii.*

Differs from *elegans* in dark, grayish brown ground color on body and top of head (superimposed black spots are distinct in some specimens), as opposed to darker, nearly black ground color of *elegans,* which obscures superimposed black spots; in fewer gastrosteges and urosteges (see pp. 34, 35); in greater average length of "6th" scale row, which is continuous from head posteriorly beyond mid-body (except for a short distance in neck region, in some specimens) as opposed to frequent reduction or absence in *elegans;* in tendency toward reduction of supralabials to 7 pairs, and of infralabials to 9 pairs, as opposed to more stable labial formula of *elegans*—8 pairs of supralabials and 10 pairs of infralabials; probably in smaller average size.

Differs from *vagrans* in darker ground color, grayish brown, as opposed to paler, buffy brown ground color of *vagrans;* in conspicuous, distinctly yellow dorsal stripe, as opposed to narrower, dull brownish, sometimes interrupted stripe; in pale, whitish supralabials, which contrast sharply with dark dorsal ground color, as opposed to brownish supralabials of *vagrans,* which nearly match brown dorsal ground color; in lack of black dots on chin and labial plates, whereas such dots are often present in *vagrans;* in immaculateness or slight spotting of ventral surface, as opposed to usual heavy black marking or spotting in *vagrans;* in pale, sharply defined lateral stripe, as opposed to dull, often faint, lateral stripe of *vagrans;* in smaller number of gastrosteges and urosteges than in typical *vagrans* (see pp. 11, 12); in tendency toward reduction of supralabials from 8 pairs to 7 pairs, and of infralabials from 10 pairs to 9 pairs.

Differs from *hammondii* in dark olive ground color; in well-developed, bright yellow dorsal stripe, vestigial or lacking in *hammondii;* in less conspicuous, often dull-colored parietal spots, as opposed to bright yellow spots of *hammondii,* which are edged with black; in blunt, shallow, irregularly shaped supralabial wedge marks, which do not extend downward to edge of mouth, as opposed to deep, slender, regularly arranged wedge marks in *hammondii,* extending to edge of mouth; in having iris dark and heavily pigmented rather than pale yellowish and almost uniformly colored; in small eyes, as opposed to large eyes of *hammondii,* which usually protrude beyond profile of labials as seen from dorsal view; in broader head and blunter muzzle, as opposed to narrow head and pointed muzzle of *hammondii;* in subequal anterior and posterior genials, as opposed to elongate posterior genials of *hammondii;* in large size and swollen appearance of posterior supralabials, as opposed to small posterior supralabials in *hammondii;* in nearly vertical suture separating 6th and 7th supralabials, as opposed to oblique, anteriorly slanting suture in *hammondii,* passing across eye, if projected.

Remarks on nomenclature and systematics.—Van Denburgh (1896:1007) included the original specimens of this form under the name *hammondii,* but commented on their different coloration. Later, Van Denburgh and Slevin (1918:244) recognized these specimens as distinct from *hammondii,* but confused them with *vagrans* and remarked: "They constitute by far the most southern record for this subspecies [*vagrans*] and offer an interesting problem in distribution, for *T. o. vagrans* has never been taken in southern California." In a later publication (1923:2), the same authors, with more specimens, described *hueyi* as a distinct subspecies and diagnosed it as "Similar to *T. o. vagrans* but with dorsal spots and dark gastrostege markings less evident and gastrosteges fewer."

Actually, *hueyi* is related to *vagrans* only through *elegans.* I think it is an isolated and only slightly differentiated southern remnant of that subspecies.

The southernmost occurrences of *elegans* are recorded from southwestern San Bernardino County in the vicinity of Big Bear Lake. It has never been authentically recorded from the San Jacinto Mountains, nor from San Diego County. Klauber's records (1929:19) of *elegans* from San Diego County are based on specimens of forms other than *elegans,* as suspected by Klauber (*in litt.*) and verified by me. Obviously these specimens were mislabeled with respect to locality by the collector; hence there is a gap of about 150 miles between the ranges of *hueyi* and *elegans.*

The San Bernardino, Santa Rosa, San Jacinto, Cuyamaca, and San Pedro Mártir ranges form a nearly continuous mountain mass, the main axis of which roughly parallels the coast line of southern California and northern Lower California. The breaks separating the various ranges of this mountain mass are not extensive, and in the past have not formed effective barriers to boreal vertebrates, many of which occur in suitable habitats on these ranges though absent from lower areas intervening.

In the cooler and more humid climate which formerly prevailed in southwestern California, boreal forms probably had wider ranges than they now occupy, and *elegans* may have occurred continuously from the Sierra Nevada south through the Sierra San Pedro Mártir. As has been shown, there is progressive decrease in the number of gastrosteges and urosteges toward the southern part of its range, and *hueyi* represents the extreme of this tendency. Probably this reduction in number of ventrals is correlated with reduction in body size. Though the number of adult specimens of *hueyi* is not sufficient to show its average adult size, all are small. *T. o. elegans* is largest in the northeastern part of its range, where the maximum numbers of gastrosteges and body scale rows occur; in the San Bernardino Mountains it averages much smaller.

Geographic variation and intergradation.—In number of gastrosteges *hueyi* is well set off from *elegans,* though there is some overlapping (see p. 34). In other characters the two forms are so similar that unlabeled specimens of *hueyi* mingled with series of *elegans* probably would not be recognized. No geographic variation within the subspecies could be shown, since all the specimens examined were collected within a small area.

Habits and habitat.—No data are available about the feeding habits of *hueyi;* probably it resembles southern populations of *elegans* in this respect, as it does in appearance and structural characters. Nothing has been published on the habitat of *hueyi.* All the known specimens were collected within a radius of a few miles in the vicinity of La Grulla and La Encantada (see pl. 1, fig. 1). The collector of the single specimen in the Museum of Vertebrate Zoölogy recorded: "... caught among rocks on side hill near meadow." This is evidence that *hueyi,* like *elegans,* is not closely restricted to the vicinity of water but may forage in dry situations. The 17 specimens of *hueyi* seen by me were collected at different times by several different collectors over a long period, but 12 specimens of *hammondii* from the vicinity of La Grulla were all collected on the same day by one collector. Therefore, I infer that *hueyi* is less restricted to a single habitat (along the edges of streams) than is *hammondii,* and that its population is less concentrated.

Where *hueyi* occurs, habitat conditions seem to parallel closely those of the

Sierra Nevada in the range of the race *elegans*. A dry open forest of yellow pine dominates the landscape. The terrain is rocky, with enormous granite boulders. A clear, swift-running stream, with but little riparian vegetation along its banks, passes down the Arroyo Encantada. At La Grulla there is a marsh and a meadow about 3 miles long. This is in high Transition Life Zone at an altitude of 7500 feet.

Records of occurrence.—Specimens examined, 17, from the following localities in northern Lower California: "San Pedro Mártir Mountains," 2 (Stanford Mus. Nat. Hist.); La Encantada, 14 (Calif. Acad. Sci., 10; Klauber, 4); La Grulla, 1 (Mus. Vert. Zoöl.).

THE ELEGANS GROUP

The Elegans group includes the four races *vagrans, biscutatus, elegans,* and *hueyi*. *T. o. vagrans* is evidently the most primitive member of this group and of the entire species. It is wide ranging and occupies an area greater than the entire area occupied by the ten other forms of the artenkreis. In scutellation and color pattern it seems to represent a central type from which all the others might have been derived. *T. o. vagrans* is less restricted to a narrow ecologic niche than is any other race of the artenkreis and is evidently primitive in feeding habits since it preys upon both terrestrial and aquatic animals.

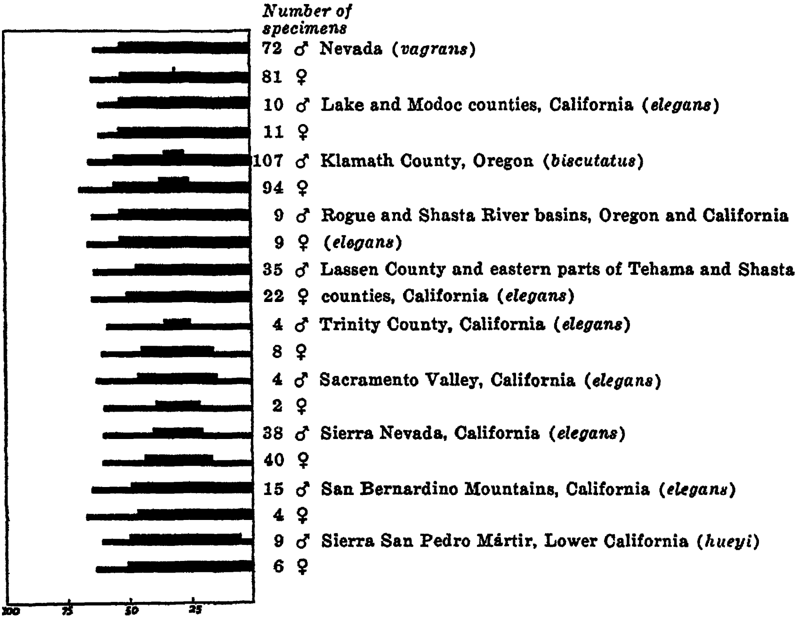

Fig. 9. Diagram showing average lengths and positions of scale rows which vary in the Elegans group (plotted for left side of body only). In each polygon longest (basal) portion represents "4th" scale row, second column represents "6th" row, and third or uppermost column (if present) represents "5th" row. Right-hand margin of figure represents head ends of snakes, and left-hand margin of figure represents posterior ends of body. Note that partly suppressed rows center at a point approximately one-third the distance from anterior end of body to anus, that all series show sexual dimorphism in having longer rows in females than in males, and that each row is longest in *biscutatus* and shortest in *elegans* from the Sierra Nevada, Sacramento Valley, and coast ranges.

T. o. biscutatus is closely related to *vagrans* but has differentiated in an isolated drainage basin (Klamath). Its more aquatic habits may be correlated with the extensive and permanent water supply in the region that it inhabits. Its large size and thick body, accompanied by increase in numbers of gastrosteges and scale rows, are also probably results of aquatic specialization. Like other members of the Elegans group, *biscutatus* has a distinct yellow dorsal stripe.

TABLE 1

NUMBERS OF PREOCULAR SCALES IN POPULATIONS OF THE ELEGANS GROUP

[Note that preoculars are undivided (total of 2) in the majority of individuals of most populations, but that in *vagrans* in the northwestern part of its range, in *biscutatus*, and in *elegans* from the region of Smoke Creek, the preoculars are frequently divided (total of 3 or 4). Preoculars are consistently undivided in *elegans* from the southern part of its range, and in *hueyi*, but no population consistently shows 4 preoculars in all specimens.]

Population	Number of specimens	Number of preoculars		
		2	3	4
B. C. (*vagrans*)	15	.60	.07	.33
NW Wash. (*vagrans*)	20	.25	.10	.65
E Wash. (*vagrans*)	17	.76	.24	—
Alberta (*vagrans*)	14	.93	—	.07
Mont., Wyo., and So. Dak. (*vagrans*)	302	.93	.07	—
Idaho (*vagrans*)	49	.90	.06	.04
Utah (*vagrans*)	57	.91	.07	.02
Colorado (*vagrans*)	58	.90	.02	.08
Ariz. and N. M. (*vagrans*)	25	.88	.04	.08
E Ore. (*vagrans*)	39	.72	.18	.10
Nevada (except Washoe Co.) (*vagrans*)	138	.84	.09	.07
Washoe Co., Nev. (*vagrans*)	18	.67	.28	.05
Smoke Cr., Calif.-Nev. line (*elegans*)	17	.24	.18	.58
Lassen and Modoc cos., Calif. (*elegans*)	32	.97	.03	—
Klamath Lake basin (*biscutatus*)	141	.53	.16	.31
SW Ore.; Siskiyou, Shasta, and Trinity cos., Calif. (*elegans*)	30	1.00	—	—
Sacramento Valley (*elegans*)	13	.92	.08	—
Sierra Nevada (*elegans*)	58	1.00	—	—
San Bernardino Mts. (*elegans*)	47	.83	.13	.04
Sierra San Pedro Mártir (*hueyi*)	15	1.00	—	—

T. o. vagrans is replaced along the western edge of its range by *elegans*. *Elegans* is typically a mountain form; its habitat is in a more humid region than that of *vagrans* and it tends to be more terrestrial in habits. Most of its food is obtained on land rather than in the water. Other garter snakes, of more aquatic habits, occur throughout most of its range, and the competition of these aquatic forms may be an important factor tending to limit *elegans* to a terrestrial habitat. In that part of its range in which the Hydrophila group does not occur, *elegans* is more aquatic. It is relatively slender, and is capable of rapid locomotion in a terrestrial environment. Its head is short and wide with a blunt muzzle; its color pattern consists of a bright yellow, sharply defined dorsal stripe which contrasts with the black ground color. The number of scale rows tends to be reduced as compared with the closely related forms, *vagrans* and *biscutatus*. Although 21 rows are usually present, one pair is of irregular length, averaging much shorter than in other members of the Elegans group, and apparently it is in the process of being lost.

TABLE 2

NUMBERS OF SUPRALABIALS IN POPULATIONS OF THE ELEGANS GROUP

[Note that 16 (8 pairs) is the usual number in most populations and is rarely exceeded, but that in occasional individuals the number is reduced to 7 on one or both sides, and that this variation is particularly common in *hueyi* and in *vagrans* in the region of Alberta.]

Population	Number of specimens	Number of supralabials					
		13	14	15	16	17	18
Ore., and Siskiyou Co., Calif. (*elegans*)	18	—	—	.06	.94	—	—
Shasta, Tehama, and Trinity cos., Calif. (*elegans*)	17	—	—	—	1.00	—	—
Lassen Co., Calif. (*elegans*)	31	—	—	—	.97	.03	—
Sierra Nevada (*elegans*)	91	.01	.01	.03	.91	.02	.02
San Bernardino Mts. (*elegans*)	41	—	—	.02	.98	—	—
Sierra San Pedro Mártir (*hueyi*)	17	—	.11	.24	.65	—	—
Lake Co., Ore., and Modoc Co., Calif. (*biscutatus*)	13	—	—	.08	.92	—	—
Klamath Lake basin (*biscutatus*)	238	—	.02	.05	.92	.01	—
B. C. (*vagrans*)	21	—	—	.10	.90	—	—
Alberta (*vagrans*)	14	—	.28	.36	.36	—	—
NW Wash. (*vagrans*)	20	—	.05	.05	.90	—	—
E Wash., Ore., Idaho, Mont., and Wyo. (*vagrans*)	174	—	.03	.11	.86	—	—
Nev. (*vagrans*)	204	—	.01	.07	.92	—	—
Col. and Utah (*vagrans*)	111	—	.05	.14	.81	—	—
N. M. and Ariz. (*vagrans*)	25	—	—	.07	.86	.07	—

T. o. hueyi, of the Sierra San Pedro Mártir in Lower California, is an isolated and only slightly differentiated race of the *elegans* stock. It differs from *elegans* mainly in having fewer gastrosteges and urosteges; hence it merely represents an extreme of a tendency, found throughout the range of *elegans*, toward reduction in number of scales farther south.

In general, members of the Elegans group are characterized by the possession of 8 pairs of supralabials and 10 pairs of infralabials; not fewer than 21 scale rows (except rarely in *elegans*); a broad flat head; a blunt muzzle with the internasals broadly in contact with the rostral, their combined contacts exceeding the contact of either nasal with rostral; swollen posterior supralabials covering large salivary glands; a distinct yellow dorsal stripe extending the full length of the body; relatively small eyes; dark, heavily pigmented iris; large pupil; and no red in the coloration.

The Elegans group is less stable in its characters than either the Hydrophila or the Ordinoides groups. Although all four of its subspecies are obviously closely related, there is much variation in habits, even within the single race *elegans*. Within this group progressive trends are less apparent than in the Hydrophila and Ordinoides groups; the four races show only slight divergent specialization.

TABLE 3

NUMBERS OF INFRALABIALS IN POPULATIONS OF THE ELEGANS GROUP

[Note that 20 (10 pairs) is the most frequent number in all groups, that this number is seldom exceeded, that occasional individuals have the number reduced to 9 on one or both sides, and that this variation is particularly common in *hueyi* and in *vagrans* from the region of Alberta (thus paralleling geographic variation in numbers of supralabials; see table 2).]

Population	Number of specimens	Number of infralabials							
		17	18	19	20	21	22	23	24
Ore., and Siskiyou Co., Calif. (*elegans*)	18	—	—	.22	.72	.06	—	—	—
Shasta and Tehama cos., Calif. (*elegans*)	7	—	—	—	1.00	—	—	—	—
Trinity Co., Calif. (*elegans*)	10	—	.10	.20	.60	.10	—	—	—
Lassen Co., Calif. (*elegans*)	31	—	—	—	.94	.06	—	—	—
Sierra Nevada (*elegans*)	105	—	.04	.08	.84	.02	.02	—	—
San Bernardino Mts. (*elegans*)	45	—	.02	.07	.91	—	—	—	—
Sierra San Pedro Mártir (*hueyi*)	15	—	.07	.40	.53	—	—	—	—
Lake Co., Ore., and Modoc Co., Calif. (*biscutatus*)	12	—	—	.08	.92	—	—	—	—
Klamath Lake basin (*biscutatus*)	235	—	.03	.05	.91	.01	—	—	—
B. C. (*vagrans*)	21	—	—	.05	.95	—	—	—	—
Alberta (*vagrans*)	14	.07	.36	.07	.50	—	—	—	—
NW Wash. (*vagrans*)	20	—	.05	.15	.70	.10	—	—	—
E Wash., Ore., Idaho, Mont., and Wyo. (*vagrans*)	119	.01	.01	.08	.84	.05	.01	—	—
Nev. (*vagrans*)	176	.01	.03	.08	.81	.04	.01	.01	.01
N. M. and Ariz. (*vagrans*)	28	.04	—	.14	.79	.04	—	—	—
Col. and Utah (*vagrans*)	108	—	.02	.09	.80	.09	—	—	—

However, definite geographic trends in scalation can be traced even within the race *elegans*. Gastrosteges are most numerous in the east-central part of its range, but undergo progressive decrease farther south. This tendency culminates in the isolated population of the Sierra San Pedro Mártir in Lower California, which is separated subspecifically mainly on the basis of its fewer gastrosteges, since it resembles *elegans* closely in other respects. It is sharply set off from typical *elegans* of the northern Sierra Nevada, but not from the nearest population of *elegans* in the San Bernardino Mountains. All specimens examined of *hueyi,* and of *elegans* from the San Bernardino Mountains region, were of small size, and it seems probable that reduction in numbers of gastrosteges is accompanied by, and correlated with, decrease in size. This stunting may result from relatively unfavorable climatic conditions at the periphery of the range.

The same tendency is found in *vagrans,* in which specimens from the extreme northern and southern part of the range have fewer gastrosteges and are of smaller size as compared with those from the central part of the range. Another possible factor having to do with dwarfing of *vagrans* in the south is the small size of streams and the isolation of drainage basins there. The aquatic fauna of these small drainage basins is poorer in numbers of species and consists of smaller animals than the faunas of more extensive northern river systems. The small size of individuals in southern populations of *vagrans* may reflect small size of available prey.

Thamnophis ordinoides hydrophila Fitch
(Oregon Gray Garter Snake, Water Snake, Moccasin)

[?] *Eutaenia vagrans,* Townsend, 1888: 240 (part)
Thamnophis vagrans, McLain, 1899: 12 (part)
Thamnophis ordinoides atratus, Van Denburgh and Slevin, 1918: 224 (part)
Thamnophis ordinoides biscutatus, Van Denburgh and Slevin, 1918: 245 (part)
Thamnophis ordinoides hydrophila Fitch, 1936: 648 (original description)

Type.—Adult male, Mus. Vert. Zoöl. No. 18127; collected at Trail Creek 6 miles from its mouth, Jackson County, Oregon, July 27, 1934, by H. S. Fitch.

Range.—Southwestern Oregon and northwestern California, from the Umpqua River on the north, southward along the coast to the Gualala River, Sonoma County, California, eastward to the Cascade Mountains in Oregon, through Shasta Valley, and into the Sacramento Valley on west side of the Sacramento River in California (see fig. 10).

Diagnosis.—Maximum number of scale rows on body 21, often reduced to 19, or, when 21 are present, the 5th reduced in length, not continuous posteriorly from head back to midbody; supralabials 8, 8; infralabials 10, 10; preocular usually single, sometimes divided; dorsal stripe dull yellow, sometimes entirely absent; area between dorsal and lateral stripes bluish gray or sometimes brownish gray, with a checkered pattern of two rows of alternately placed black blotches on each side; supralabials dusky superiorly, pale inferiorly, marked posteriorly with slender, black wedge marks which continue downward to edge of mouth; top of head mainly gray; parietals and frontals marked with black; postoculars dull colored, not sharply contrasting with surrounding scales; chin white; ventral surface immaculate or nearly so, with pink or purplish suffusion of scales posteriorly; posterior supralabials relatively small; contact of each nasal with rostral usually exceeds combined contact of both internasals with it; head elongate and narrow posteriorly; iris uniformly gray or brown; pupil relatively small.

Coloration.—Description of type (made before preservation).

Top of head Drab, mottled with black on prefrontals, frontal, supraoculars, and parietals; black predominates posteriorly; supralabials pale, nearly white on their lower parts, dusky above, predominantly Light Olive-Gray, margined posteriorly with black which forms slender, triangular wedge marks, apices reaching or approaching edge of mouth; side of head above supralabials dull gray with no contrasting markings; iris uniformly Cinnamon-Rufous; dorsal stripe Avellaneous, broader and more distinct in neck region than posteriorly on body, and with skin betwen scales at its anterior end faintly tinted with orange; stripe involves only a portion of middorsal scale row for most of its length; dark dorsolateral spots Chaetura Drab, lighter areas separating spots Deep Olive-Gray; pale flecks arranged in transverse rows on these lighter areas, nearly white, with faint bluish tint on anterior part of body, those on posterior part of body Light Ochraceous-Buff; chin white; ventral surface of body purplish tinted, increasingly so posteriorly, Vinaceous-Tawny where most highly colored at posterior end of body and base of tail; gastrosteges iridescent, each margined with black anteriorly (apparent only when skin is stretched), and with irregular black markings on their centers, most pronounced in those about 20 gastrosteges anterior to anus; no black visible on first 10 gastrosteges except when skin is stretched; lateral stripe pale gray, not distinctly set off from color of ventral surface, many scales at its anterior end behind corner of mouth tinted with Apricot Orange, which is present in limited amount along lateral stripe for most of its length, though not conspicuous.

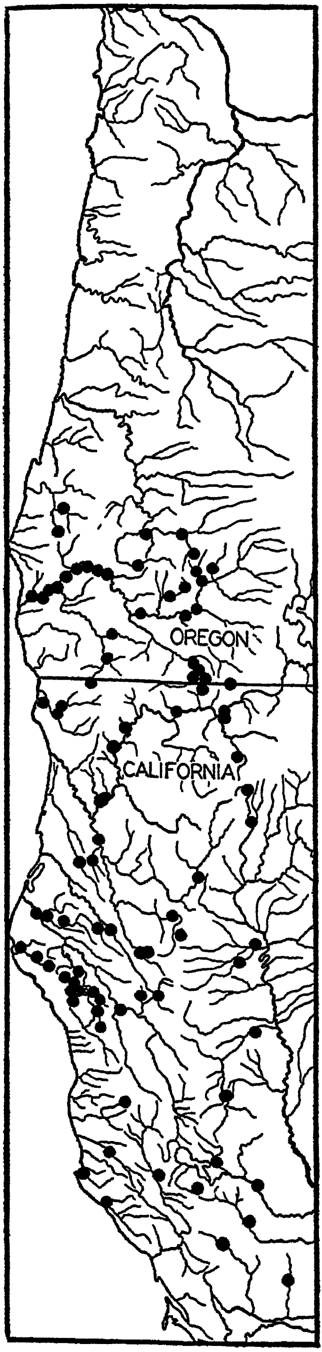

Fig. 10. Range (localities of specimens examined) of *Thamnophis ordinoides hydrophila* in southwestern Oregon and in California south to the San Francisco Bay region.

Comparisons.—Because this subspecies shares parts of its geographic range with *T. o. ordinoides*, *atratus*, and *elegans*, and because it intergrades with *couchii*, the most closely related race, and with *biscutatus*, comparisons are made with each of these forms. Comparison with *couchii* will be found under discussion of that race.

Differs from *ordinoides* in color (usually dull tan) and narrowness of dorsal stripe (except in Trinity and eastern Mendocino counties), as opposed to usually distinct red, yellow, or orange dorsal stripe of *ordinoides;* in pale, gray, ground color with usually conspicuous checkered pattern, as opposed to usually brown or sometimes black ground color of *ordinoides,* which ordinarily lacks conspicuously checkered pattern because of small size of superimposed black spots; in uniformly brown or gray iris, as opposed to dark iris in *ordinoides*, which is heavily clouded with pigment granules but has pale, yellowish, inner rim encircling pupil; in absence of bright red spots and presence of pinkish or purplish suffusion on ventral surface, as opposed to frequent irregular bright red spotting of gastrosteges and urosteges, and lack of pinkish suffusion ventrally in *ordinoides;* in narrowness of muzzle and distinctness of head from neck, as opposed to blunt muzzle of *ordinoides* and narrowness of head in temporal region (not distinctly set off from neck); in greater numbers of gastrosteges and urosteges (little overlapping in numbers if sexes are compared separately, see pp. 84, 105); in 8 supralabials and 10 infralabials on each side as opposed to 7 pairs of supralabials and 9 or 8 pairs of infralabials in *ordinoides;* in frequent possession of "6th" scale row on body (making total of 21 rows), and continuance of "4th" row posteriorly beyond mid-body, as opposed to absence of "6th" row, and usual absence or marked shortening of "4th" row in ordinoides; in larger size (see p. 8).

Differs from *atratus* in narrow, and dull rather than bright lemon yellow, dorsal stripe, which in *atratus* involves at least middorsal scale row and half of each row on either side; in absence of red markings on ventral surface, dorsolateral area, or (with rare exceptions) on lateral stripe, as opposed to color pattern in *atratus* in which ventral surface, dorsolateral area, or lateral stripe may be extensively marked with red; in pinkish suffusion of ventral surface, as opposed to lack of such suffusion and frequent medial blotching with pink or yellow in *atratus;* in uniformly brown or gray iris, as opposed to greenish gray iris in *atratus* (heavily pigmented like that of *ordinoides* in northern part of its range); in pointed muzzle (nasorostral contact usually exceeding contact of both internasals with rostral), as opposed to blunt muzzle of *atratus* (nasorostral contact is usually exceeded by combined contact of internasals with rostral); in relatively long posterior genials as opposed to usually subequal genials; in paler ground color; in having slender wedge marks along posterior edges of supralabials, whereas such marks are not usually developed in *atratus;* in small posterior supralabials, and anteriorly slanting suture between 6th and 7th, as opposed to larger supralabials of *atratus,* 6th and 7th separated by more nearly vertical suture; in larger eye.

Differs from *elegans* in dull, indistinct dorsal stripe, as opposed to bright lemon yellow stripe of *elegans;* in gray ground color, as opposed to black ground color in *elegans;* in small posterior supralabials, somewhat suffused with brown or gray, each marked posteriorly with a slender black wedge mark which extends downward to edge of mouth, as opposed to large and swollen posterior supralabials in *elegans,* which are pale, nearly white, and marked posteriorly with wider wedge marks which do not extend downward to edge of mouth; in having suture separating 6th and 7th supralabials slanting forward, and rounded at its upper end (thus convex posteriorly), as opposed to more nearly vertical suture of *elegans,* which is usually slightly concave posteriorly; in narrow, pointed head, as opposed to broad, triangular head and blunt muzzle in *elegans;* in pale, uniformly colored iris, as opposed to dark brown, heavily pigmented iris with pale narrow rim encircling pupil in *elegans;* in fewer gastrosteges and urosteges; in relatively longer posterior genials, as opposed to subequal genials of *elegans.*

Differs from *biscutatus* in dull, indistinct dorsal stripe, as opposed to distinct lemon yellow or even orange yellow stripe of *biscutatus* (which, however, is somewhat suffused with dusky ground color); in pale gray or brown ground color, conspicuously checkered with black spots, as opposed to dark, nearly black ground color of *biscutatus,* which obscures superimposed spots; in restriction of black on top of head to parietal region, as opposed to more extensive black markings on head of *biscutatus,* encroaching on supraoculars and frontal; in more pointed muzzle; in absence of "5th" scale row and absence or marked reduction of "6th" row, as opposed to frequent possession of "5th" row and posterior extension of "6th" row beyond mid-body in *biscutatus;* in having one preocular on each side, as opposed to frequent division of preoculars into three or four separate scales in *biscutatus;* in fewer gastrosteges and urosteges.

Remarks on nomenclature and systematics.—The subspecies *hydrophila* is in some respects transitional between *couchii* and *biscutatus,* with which it intergrades in different parts of its range. Before the present study was undertaken, few typical specimens of this form had been collected. Van Denburgh and Slevin did not recognize it as distinct, but they were confused by the few specimens available to them; they classified some as *biscutatus* and listed others as *atratus.* Under their discussion of *biscutatus* these authors remarked (1918:251): "It seems best to include here also the snakes from Del Norte County [Gasquet], California, and from Josephine [Grants Pass] and Coos [South Fork of Coquille River, 20 miles above Myrtle Point] counties, Oregon, although the number of specimens is so small as to leave one in doubt as to the usual number of preoculars and the coloration is more like that of *T.o. couchii.*" Though one specimen from Gasquet (Stanford Mus. Nat. Hist. No.

4264) was listed under *biscutatus* by them, a second from this same locality was classified as *atratus*. One from Carlotta (Calif. Acad. Sci. No. 28889) and two from Alton (Calif. Acad. Sci. Nos. 28977 and 28979) were collected along with large series of *atratus* and were classified with them by Van Denburgh and Slevin. Two from "near Siskiyou," Jackson County, Oregon (Stanford Mus. Nat. Hist. Nos. 4440 and 4442), which show intergradation between *hydrophila* and *biscutatus,* were classified by Van Denburgh and Slevin as *atratus,* but were mentioned as probably showing intergradation between *atratus* and *elegans*. As I have indicated elsewhere (Fitch 1936:650), it is highly improbable that these specimens were collected on the north slope of the Siskiyou Mountains where Siskiyou Station is situated. Probably they were collected in the drainage of Cottonwood Creek, a tributary of the Klamath River, where a specimen of similar appearance was secured by me in 1934.

Van Denburgh and Slevin (1918:233) wrote regarding the five specimens of *hydrophila* in the Stanford Museum of Natural History collection, from the Coquille River 20 miles above Myrtle Point, Coos County, Oregon, which they classified as *biscutatus:* "They, however, are not typical of that form in that they have only nineteen rows of scales. They thus resemble *atratus* in this character and might well be regarded as intergrades. Additional specimens are needed from this general region. The coloration of these specimens is similar to that of *T. o. couchii* in the indistinctness of the dorsal line and presence of dark pigmentation on the gastrosteges."

In discussing intergradation between *ordinoides* and *atratus,* Van Denburgh and Slevin (1918:223) commented: "South of Del Norte County no tendency toward *T. o. ordinoides* has been observed in *T. o. atratus* unless it be that the rather frequent absence of the dorsal line in specimens from Humboldt and Mendocino counties may be so regarded." The specimens referred to proved to be *hydrophila*.

In its geographic distribution *hydrophila* coincides roughly with the area occupied by the "Klamath Mountain" system (Jepson, 1925:10) of northwestern California and southwestern Oregon, including the Yolla Bolly, Scott, Salmon, Marble, and Siskiyou mountain ranges. This region is characterized by metamorphic rocks, mainly schists and granites, older and harder than the rocks found in most of the coast ranges, and predominantly gray, of probable significance in relation to the gray ground color of *hydrophila*. Throughout its range *hydrophila* is closely restricted to streams having rocky beds. On the north its range extends into the Umpqua drainage basin. More collecting is needed to establish its exact northern limits. However, it probably does not extend northward into drainage basins beyond that of the Umpqua River, although there are no high mountain ranges or other obvious physical barriers to prevent such distribution. Rather, the coast ranges there are low; the region is characterized by heavy rainfall, and there are many large, slow-moving streams. Vegetation is luxuriant in this humid climate. Under such conditions no suitable habitat for these snakes exists. In the slowly moving, deep water of the streams there are few protruding boulders such as would offer favorable basking places in swifter water courses. The banks are overgrown with dense vegetation overhanging the edges of the streams, and there are no marginal areas of bare rocks and boulders such as characterize many of the swifter streams to the southward. Under such habitat conditions, which prevail along the Siuslaw River and along other coastal streams to the northward, the ecologic niche of *hydrophila* does not exist.

Along many coastwise streams *hydrophila* has been taken within a few miles of the ocean, although it is more abundant farther inland, where the streams are swifter, with more exposed rocks, and where marginal streamside vegetation is less dense. The Pacific Ocean thus demarcates the western limit of its range. Intergradation with *couchii* takes place at the north end of the Sacramento Valley where ranges of the two forms meet. On the northeast its range is limited by the Cascade mountain chain rising to unfavorably high altitudes, and beyond it by the arid Great Basin region where its habitat does not exist. In the Klamath Lake region *biscutatus* replaces it ecologically, and where the Klamath River cuts through the Cascades the two forms meet and intergrade. Thus the competition offered by *biscutatus,* presumably better adapted to conditions existing in the Klamath Lake region, is a limiting factor to its eastward distribution. From the Klamath River southward, high mountains form a continuous barrier along the east side of Shasta Valley and beyond to the Pit River where *hydrophila* is replaced by *couchii.*

Geographic variation and intergradation.—In the Rogue River and Umpqua River basins *hydrophila* has a dorsal stripe which is dull, pale brown, or cream color, and often indistinct except on the anterior part of the body. The lateral stripe is often indistinct: its scales are suffused with the dusky ground color except along their edges. The checkered pattern of dorsolateral spots is usually conspicuous, though in some specimens from the coastal region these spots are reduced in size so that their corners do not overlap. The ventral surface is usually tinted with pink or purple, and shows a wide range in the extent and intensity of this coloring, which disappears entirely in preservative. The parietals are mainly black, and the posterior portions of the supraoculars and frontals are usually marked with black also. There is much individual variation in scale characters in specimens from this region. The "6th" scale row may be entirely absent, or it may be continuous from head back to mid-body; in most specimens it is present for a short distance on the anterior part of the body. It is best developed in specimens from the Umpqua basin, somewhat reduced in those from the Rogue River basin, and more reduced in those from the lower Klamath River (Bluff Creek, Blue Creek, Dillons Creek, Clear Creek), which are, however, indistinguishable from typical *hydrophila* in general appearance. In specimens from localities farther south and west the "6th" scale row is altogether wanting.

Specimens from more eastern localities within the Klamath drainage (Horse Creek, Beaver Creek, Shasta River) show progressive increase in extent of the "6th" scale row, but they differ from typical *hydrophila* in coloration; the ground color becomes darker, so that the dorsolateral spots are less noticeable; the dorsal stripe is wider, more distinct, and yellower. The lateral stripes are more distinct, brightly tinted with pink or orange. The ventral surface is also brightly colored, pink or ochraceous. Black coloring on top of the head extends farther forward than in typical *hydrophila* and usually involves most of the frontal and supraocular plates. The unusually bright tints of the lateral stripes and ventral surface seem to be peculiar to specimens from this region, but in other color characters they approach *biscutatus,* and some of those seen by me in life at the mouth of the Shasta River were indistinguishable from typical *biscutatus* on the basis of color characters. They show further resemblance to *biscutatus* in often having preoculars divided on one or both sides. These specimens have more elongate pointed muzzles as compared with *biscutatus,* showing affinity to *hydrophila* in this respect. They show intergradation between *biscutatus* and *hydrophila* in all characters which separate the two forms, but are classified as *hydrophila* because none has a "5th" scale row (making a total of 23 on the body), the "6th" row is usually reduced as compared with that of *biscutatus,* and average numbers of gastrosteges and urosteges are nearer the numbers found in typical *hydrophila* than the numbers in typical *biscutatus.* Individuals collected or seen along the Shasta River at Parks Creek, and two miles north of Yreka, had a paler ground color than those from nearer the mouth of the river, thus resembling *biscutatus* less closely in coloration.

Specimens from Smith River, Del Norte County, differ from typical specimens in being paler gray with dorsolateral spots reduced in size and well separated.

Specimens from Willow Creek, a tributary of the Trinity River and hence in the Klamath River drainage, in northeastern Humboldt County, differ from typical *hydrophila* in having more distinct stripes. The dorsal stripe is distinctly yellowish and is widened to include adjacent parts of the scales on either side of the middorsal row for the full length of the body. Scales of the lateral stripes have but little dusky suffusion and are pale, contrasting with the shades of the ventral surface and of the dorsolateral area. This contrast is heightened by the coloration of the dorsolateral area, which is so dark that the superimposed spots are obscured. At its anterior end the lateral stripe extends dorsally to involve the scale above and behind the last supralabial, which is normally dull colored in typical *hydrophila.*

Specimens from Trinity County differ markedly from typical *hydrophila* in having the dorsal stripe wider, yellower, and more distinct, and in having the dorsal ground color darker. This is especially true of specimens taken in the western and central parts of the county near Hayfork and Forest Glen. Five from Trinity River south of Trinity Center show a wide range of variation; they approximate the typical color pattern at one extreme, and at the other resemble distinctly striped specimens from western Trinity County. However, the lateral stripe is conspicuously developed in all; it involves the scale above and behind the last supralabial.

In specimens from the upper Sacramento River (near Dunsmuir and at Shotgun Creek) the dorsal stripe is pale, but is distinct and yellowish without noticeable dusky suffusion; the lateral stripe is also well developed and involves the scale above and behind the last supralabial. These specimens have

21 rows of scales for a short distance on the anterior portion of the body and seem to show intergradation with *couchii* in this character.

Specimens from the west side of the Sacramento Valley from Cottonwood Creek (south fork, and at Cottonwood), Stony Creek (Stonyford and Orland), and Cache Creek (near Stubbs and at Rumsey) are similar in appearance except that their dorsal stripes are fainter and their body spots are reduced in size. They resemble *couchii* in having a "6th" scale row (which, however, is of variable length and usually short) on the anterior part of the body.

In a series from Redwood Creek, Humboldt County, the dorsal stripe is reduced, suffused with dusky coloring, and, in some, hardly discernible, although there is wide individual variation. The lateral stripe is correspondingly faint; its scales are bluish gray and do not contrast with the color of the ventral surface. In the majority the parietals are mainly or entirely black and this color extends anteriorly on to the frontal and supraoculars, but in some the black is confined to a narrow margin bordering the parietal spots and to the edges of the suture between the two parietal plates. The ground color is darker than in typical specimens, and the dorsolateral spots are large, so that their corners tend to overlap. The supralabials are pale on their lower portions.

In specimens from the Mattole River, Humboldt County, the dorsal stripe is faint and usually confined to the anterior part of the body. The dorsolateral spots are smaller than in typical *hydrophila,* and they tend to be broken up by brown areas on the centers of the scales. The lateral stripe is faint with dusky suffusion; it does not involve scales above the corner of the mouth. The ground color is brownish, less gray than in typical *hydrophila.* In Mus. Vert. Zoöl. No. 18728 there is no black on top of the head and in most of the others the black is confined to the median portions of the parietals, hence less extensive than in typical specimens. Series from the south fork of the Eel River are similarly colored. Several of them are peculiar in having small rusty red spots on a few of the dorsal scales, or on the lateral stripe.

In western Trinity County and eastern Mendocino County a population of *hydrophila* exists which is so different from typical populations in appearance that it might be considered worthy of recognition as a distinct subspecies. It has here been tentatively retained within the subspecies *hydrophila,* partly because its range as a distinct race cannot yet be defined accurately. However, a center of differentiation is apparent. Snakes from this differentiation area, which includes the basins of the middle fork of the Eel River, Rattlesnake Creek in northern Mendocino County, and the upper Mad River, approach *T. o. elegans* in coloration. The dorsal ground color is dark, almost black; the dorsal stripe is bright yellow with scarcely a trace of dusky suffusion, and involves in addition to the middorsal scale row, the adjacent half of each row lateral to it for most of its length; the supralabials are pale; the lateral stripes are well developed with scarcely a trace of dusky suffusion. Specimens from the South Fork River near Forest Glen are of similar appearance, but the dorsal stripe is somewhat more dusky. Specimens from Willow Creek, Humboldt County, have dorsal stripes of much paler appearance and have paler ground colors; they are intermediate in coloration between typical *hydrophila* and its yellow-striped phase. Specimens from Cobbs, on the upper Van Duzen River, are likewise intermediate, but are more distinctly striped than those from Willow Creek. Specimens from Ten-mile Creek and Rattlesnake Creek, northern Mendocino County, have the dark yellow-striped pattern strongly developed. Those from the south fork of the Eel River, only a few miles farther west, are of an entirely different appearance; the ground color is dull brownish gray, and the dorsal stripe is indistinct or (rarely) lacking, and likewise the lateral stripes are faint. Transition between these color extremes takes place abruptly within a few miles, between Cummings and the mouth of Rattlesnake Creek, as shown by series of specimens collected at intervals along the creek.

The populations of *hydrophila* in the south fork of the Eel River and other coastal streams of Mendocino and Humboldt counties are identical in scalation (except for reduction of numbers of gastrosteges and urosteges in the south), with the brightly striped phase occurring farther east, despite striking color differences. This composite group, including all the *hydrophila* of Mendocino, Humboldt, and western Trinity counties, is therefore fairly uniform in scalation, but is well set off from the northern "typical" populations of *hydrophila* in lacking even a vestige of the "6th" scale row, in having fewer gastrosteges, and in having the preoculars always undivided.

To sum up the variation shown within this subspecies: Series from southwestern Oregon and northwestern California, from the Umpqua, Coos, Coquille, Rogue, Smith, and lower Klamath river basins, have dull-colored, narrow, dorsal stripes and faint lateral stripes, a pale gray ground color, large dorsolateral spots, "6th" scale row usually present on anterior part of body, preoculars sometimes divided, gastrosteges and urosteges more numerous; series from the coast of Humboldt and Mendocino counties are similar in appearance, except that the dorsal spots on the body tend to be reduced; however, they have single preoculars, lack the "6th" scale row, and show progressive decrease in numbers of gastrosteges and urosteges toward the south; series from eastern Mendocino County and from western Trinity County resemble those found farther west in characters of scalation, but they have a dark nearly black ground color and a bright yellow dorsal stripe; specimens from the Shasta River basin show intergradation with *biscutatus* in having the ground color dark, stripes well developed, preoculars usually divided, "6th" scale row extensive, numbers of gastrosteges and urosteges increased; specimens from the north and west sides of the Sacramento Valley show intergradation with *couchii* in also having increased numbers of gastrosteges and urosteges and in having the "6th" scale row extensive; they are of pale ground color, having stripes pale but distinct, and dorsal spots reduced in size.

Habits and habitat.—Of 370 snakes for which habitat data are available, 169 were recorded as seen in the water; many of these were first seen on rocks on shore, and they swam or dove to escape; others were lying in shallow water or were actively foraging among rocks on the bottom. Eight others were recorded as seen on rocks at midstream. One hundred and seventy others were found within 5 feet of the edges of streams (within 3 or 2 feet of them, usually); many of these, perhaps the majority, were also in the water or took to the water in escaping. Thirty-five more were recorded as being found on rocks at the edge of the water. Thirteen (about 3½ per cent) were found at distances greater than 5 feet from water (up to 100 yards) but some of these contained aquatic animals in their stomachs; apparently, each of these snakes had left the vicinity of water to find shelter wherein either to escape a storm, or spend the night, or to digest food which it had eaten.

Ninety-six of the specimens examined, representing 27 localities widely scattered throughout the range, had eaten a total of 139 different items. Of these items 131 were of kinds which must have been found under water by the foraging snake. The remaining were all yellow-legged frogs (*Rana boylii*), a species known to be closely restricted to the vicinity of streams; some or all of them may have been caught under water, though more probably they were caught among rocks at the edges of the streams. Fish (and their eggs) and *Rana boylii* together comprised more than 80 per cent of the food items consumed. Fish were eaten more than twice as often as *Rana boylii*, and of this species tadpoles were eaten five times as often as metamorphosed frogs. Recognizable fish remains consisted almost entirely of *Cottus* and young trout, and the former were eaten almost twice as often as the latter. Larvae of salamanders (*Triturus* and *Dicamptodon*) are occasionally eaten. These snakes partly compensate for any damage they may do in destroying trout by acting as a natural check on *Cottus*, since fish of that genus are destroyers of trout spawn and young fry. Most of the trout destroyed by *hydrophila* are young, between one and three inches in length, but many of the *Cottus* destroyed by them are adults. It is probable that fishes are seldom or never caught by the snakes in open water. The snakes forage among rocks on the bottom, and in crevices and crannies catch animals which could easily escape them in the open. *Cottus* is restricted to this gravel habitat and is therefore caught more often than trout, which spend much of the time off the bottom in the current.

This accumulated evidence indicates that *hydrophila* is closely restricted in its distribution to permanent streams having rocky beds and a flow of swift, clear water, is primarily a "water snake" ordinarily depending on the water both as a place of refuge from danger and as a source of food, is restricted to low Transition and high Upper Sonoran life zones, and occurs along streams only where there are trees and bushes near the water offering shade, but not where streams are continuously walled in by dense vegetation. Marginal streamside areas of open rocks for basking in the sunlight are necessary to it. Because of the low water temperature in streams where it occurs, continuously prolonged under-water foraging would result in much decreased activity. Except in unusually warm weather, intervals of basking are probably necessary to maintain the body temperature at a level which will allow efficient foraging. Snakes of this kind are apt to be encountered coiled on rocks at the edge of the water, and it is probable that much of the time they spend away from shelter is passed in this manner, although their actual foraging is done almost entirely under water.

Records of occurrence.—Specimens examined, 407, in the Museum of Vertebrate Zoölogy (unless otherwise indicated), from the following localities:

Oregon. *Coos County:* Coquille River 8 miles below Bridge Post Office, 1, and 20 miles above Myrtle Point, 5[3]*. *Douglas County:* Canyonville, 2[3]; Canyon Creek 1 mile south of Canyonville, 2; south fork of Umpqua River 3 miles west of Tiller, 1; Elk Creek 13.6 miles (by road) southeast of Tiller, 7; U. S. highway No. 99 at Cow Creek, 2. *Jackson County:* Trail Creek 6 miles above its mouth, 35 and 1 mile north of Trail, 21; Elk Creek 7 miles above its mouth, 2; Little Butte Creek at Rogue River, 1; Upper High Banks, Rogue River, 1; Big Applegate River at mouth of Beaver Creek, 11, at mouth of Squaw Creek, 2, and at mouth of Carberry Creek, 1; Evans Creek 7 miles northeast of Beagle, 10, and 10 miles above Wimer, 9; "near Siskiyou," 2[3]. *Josephine County:* Deer Creek, 1[3]; "Rogue River," 4[1]; Rogue River 2 miles below Almeda, 3, Rainie Falls, 10, Jackson Creek, 1, Grants Pass, 1[3], and Bunker Creek, 12. *Curry County:* Rogue River at Burns Creek, 2, Solitude Bar, 6, 2 miles west of Agness, 1, Silver Creek, 5, Lobster Creek, 2, and 11 miles from mouth, 1; Illinois River 5 miles west of Holland, 1.

California. *Del Norte County:* East fork of Illinois River at 1900 feet, 1; Smith River 5 miles above Gasquet, 3, Gasquet, 2[3], and 5 miles northeast of Crescent City, 1[2]. *Siskiyou County:* Cole, east fork of Cottonwood Creek at Oregon State line, 1; Shasta River at its mouth, 3, and 1 mile above mouth, 11; 2 miles north of Weed at Parks Creek, 1; Klamath River at Horse Creek, 10; Clear Creek, 1400 feet, 3; Sacramento River 7 miles north of Dunsmuir, 2. *Humboldt County:* Klamath River at Dillons Creek, 5, Blue Creek, 1, and Bluff Creek, 5; Trinity River 4 miles southeast of Hoopa, 1; east fork of Willow Creek, 8; Redwood Creek at Grays Resort, 19; Alton, 2[3]; Cuddabeck, 1; Carlotta, 3[3]; north fork of Mattole River at Petrolia, 1; south fork of Mattole River at Woods Creek, 19, and at Thorn, 1[3]; Briceland, 1[3], 3 miles west of Bridgeville, 1; Van Duzen River at Cobbs, 13; Garberville, 2[3]. *Trinity County:* east fork of Trinity River 12 miles south of Trinity Center, 5; Deerlick Springs, 1; 2 miles east of Forest Glen, 1; 2 miles west of Forest Glen, 1; 6 miles east of Forest Glen, 1; 6 miles east of Hayfork, 1. *Shasta County:* Sacramento River at Shotgun Creek, 1; Cottonwood, 1[3]. *Mendocino County:* south fork of Eel River ¼ mile south of Humboldt County line, 1; and 12 miles south of Garberville, 2; 9 miles west of Cummings, 29, Big Dan Creek, 14, Rattlesnake Creek at mouth of Squaw Creek, 2, Cummings, 6, 1 mile west of Cummings, 1, 5 miles southeast of Cummings, 7; Ten-mile Creek 5 miles north of Laytonville, 4; middle fork of Eel River at Jumpoff Creek, 6; ½ mile east of Dos Rios, 3, and 7 miles northeast of Covelo, 1; Sherwood, 1[3]; Bald Hill, 2; Garcia River, 2[3]; Navarro River near Philo, 4[3]; Pieta Creek, 1; Gualala, 8. *Tehama County:* south fork of Cottonwood Creek, 1. *Glenn County:* Stony Creek near Orland, 3[3]. *Lake County:* Cache Creek 6 miles east of Stubbs, 1; Glenbrook, 1[2]. *Colusa County:* 3 miles west of Stonyford, 800 feet, 1. *Yolo County:* Rumsey, 1. *Napa County:* Berryessa Creek, 4. *Solano County:* 3 miles west of Vacaville, 3.

Thamnophis ordinoides couchii (Kennicott)

(Giant Garter Snake, Water Snake, Black Water Snake, Fish Snake, Moccasin, Couch Water Snake)

Eutaenia couchii Kennicott, 1859:10 (original description)
Eutaenia Hammondii, Kennicott, 1860*b*:332 (part)
Eutaenia vagrans, Townsend, 1888:240 (part)
Thamnophis hammondii, Stejneger, 1893:212
Eutaenia elegans couchii, Cope, 1900:1042 (part)
Thamnophis hammondii, Van Denburgh, 1897:212 (part)
Eutaenia elegans vagrans, Brown, 1903:290 (part)
Eutaenia hammondii, Brown, 1903:295 (part)
Thamnophis ordinoides elegans, Ruthven, 1908:138 (part)
Thamnophis ordinoides hammondii, Grinnell and Camp, 1917:181 (part)
Thamnophis ordinoides couchii, Van Denburgh and Slevin, 1918:251 (part)
Thamnophis ordinoides atratus, Grinnell, Dixon and Linsdale, 1930:151 (part)

Type.—"Apparently female" (L. Stejneger, *in. litt.*), U. S. Nat. Mus. No. 866; from "Banks of Pit River, California" (probably near mouth of Hat Creek), collected by J. S. Newberry.

Range.—Sierra Nevada of California, along streams, mainly at middle altitudes in

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* Explanation of references: [1] University of Michigan Museum of Zoölogy; [2] California Academy of Sciences; [3] Natural History Museum, Stanford University.

Transition and Upper Sonoran life zones, from Pit River and Susan River south into Kern County at Walker Basin Creek and, formerly at least, to Fort Tejon; eastward into west-central Nevada, along Truckee River to Pyramid Lake, Carson River to Fallon, and Walker River to Yerington (see fig. 11).

Diagnosis.—Maximum number of scale rows on anterior part of body ordinarily 21 (rarely 23), the 5th (when 21 are present) continuous from head back to mid-body; supralabials 8, 8; infralabials 11, 11 (or reduced to 10 on one or both sides); preocular often divided; dorsal stripe dull yellow suffused with dusky coloring, usually absent on posterior part of body and on tail; lateral stripes distinct, dull yelllow; dorsolateral area between dorsal and lateral stripes brown with two rows of alternately placed black spots usually larger than interspaces so that their corners overlap slightly; these spots tend to be square; supralabials brownish superiorly, pale inferiorly, marked posteriorly

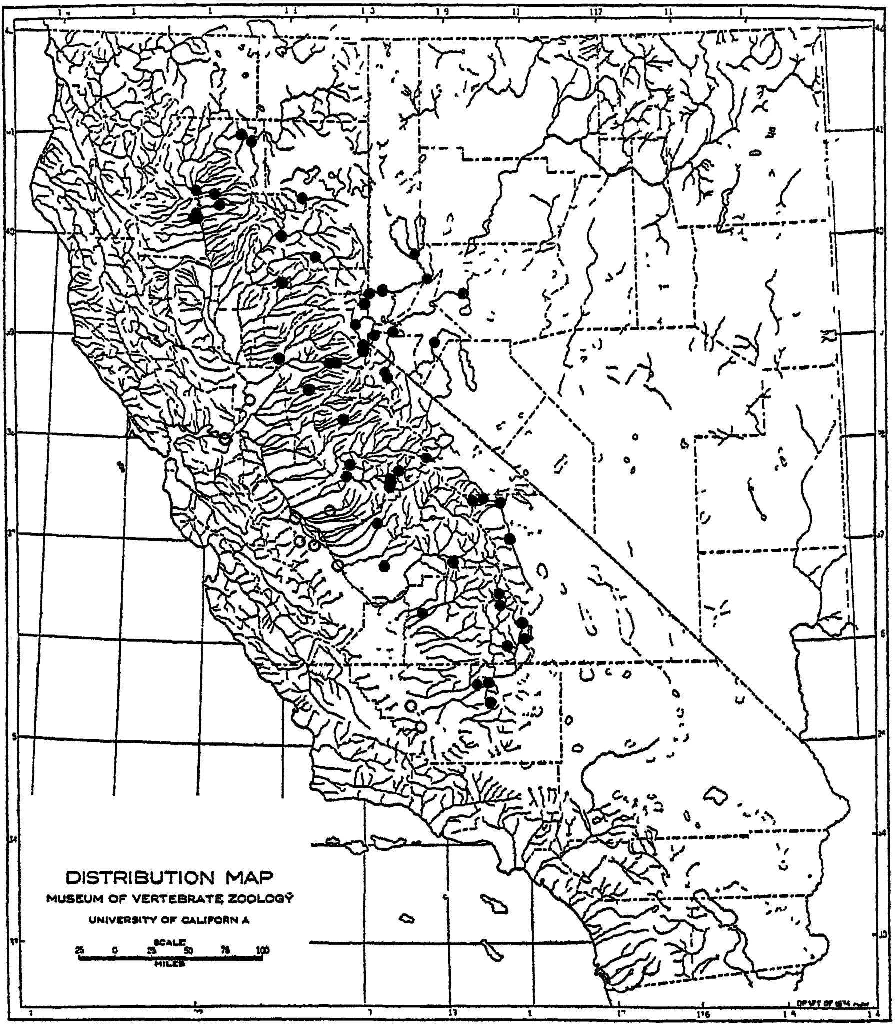

Fig. 11. Range of *Thamnophis ordinoides couchii* (dots indicate localities of specimens examined) in California and Nevada, and range of *Thamnophis ordinoides gigas* (circles) in the San Joaquin Valley of California.

with black areas which do not form typical triangular wedge marks but are elongated and may tend to form a longitudinal bar; top of head brown; infralabials and genials often marked with black; ventral surface ochraceous, often heavily marked with black; lower postocular and region behind corner of mouth pale, contrasting with dark color of other portions of head; gastrosteges average more than 176 in males and more than 172 in females, posterior supralabials relatively small, sixth often convex posteriorly and rounded on its upper hind corner; anterior height of nasal markedly exceeds combined contact of both internasals with rostral; muzzle long and pointed; head narrow posteriorly; eye relatively large, often protruding beyond profile of labials as seen from dorsal view; iris yellowish brown, pupil small, its diameter exceeded by width of iris (see pl. 5, figs. 2 and 3).

Coloration.—Description of freshly killed adult female, Mus. Vert. Zoöl. No. 19202, collected at Cromberg, middle fork of the Feather River, Plumas County, California.

Top of head Deep Olive with black superimposed on posterior part of frontal, posteromedial portions of supraoculars, and middle part of parietals; posterolateral corners of frontal yellowish; faint paired yellowish dots on frontal one-third of distance forward from posterolateral corner to anterolateral corner; supralabials Olive-Gray with vertical black marks along their posterior borders, of irregular outlines, not in the form of distinct wedge marks; posterior supralabials paler, nearly white on their lower portions but dusky with brownish suffusion on their upper portions; postocular region including extreme lower edge of upper postocular, all of middle and lower postoculars, and adjacent anterior end of anterior temporal pale yellow, contrasting sharply with darker color of top of head; scales above and behind last supralabial and two successive scales behind corner of mouth pale, matching lateral stripe and continuous with it, and contrasting sharply with black of scales above and behind; scales of head lateral to dorsal stripe and behind parietals black; preocular plate pale but with slight dusky suffusion and darker than postoculars; infralabials Olive-Gray, each margined with black posteriorly, the four posterior on each side dotted or marbled with black; parietal spots Pinard Yellow; iris Dresden Brown; dorsal stripe Citrine (near Sulphine Yellow at extreme anterior end), indistinct, mainly confined to scales of middorsal row, scarcely discernible posteriorly behind mid-body; dorsolateral area between dorsal and lateral stripe Chaetura Drab with two longitudinal rows of black spots on each side, these spots averaging one and three-quarters scales in length with intervening lighter areas usually about one-half to three-quarters the length of a single scale; light coloring mainly confined to flexible skin between scales; each scale mainly grayish brown, approximating color of dark spots but narrowly margined with paler borders where it adjoins areas of paler skin; on anterior part of body four pale skin areas partly separate each successive black spot of the lower row from the spot anterior to it, and there are three such pale skin areas separating each two successive spots of upper row; lateral stripe distinct, mainly on second and third scale rows, its scales Dark Olive-Buff and Citrine-Drab bordered on their anterolateral margins with Picric Yellow; pale flecks on dorsolateral area in two alternating rows; Martius Yellow on skin, nearer Picric Yellow where they encroach on anterolateral margins of scales; chin Ivory Yellow; gastrosteges suffused with pinkish coloring, faint anteriorly but suffused posteriorly with Orange-Vinaceous except for gray outer edges.

Comparisons.—*T. o. couchii* intergrades with the races *hydrophila* and *gigas;* its range is adjacent to that of *hammondii* and overlaps the ranges of *elegans* and *vagrans.* Comparisons with *gigas and hammondii* are made in the discussions of those forms.

Differs from *elegans* in faint, dull, dorsal stripe, narrow, and often confined to anterior portion of body or to neck region, whereas in *elegans* dorsal stripe is bright lemon yellow or orange yellow, contrasts sharply with dark ground color, and extends full length of body; in sometimes having chin and ventral surface of body blotched or heavily marbled with black, and in brown coloring along edges of gastrosteges and on infralabials, and in ventral surface suffused with ochraceous coloring posteriorly, whereas in *elegans* ventral surface is pale gray with delicate pinkish suffusion, immaculate, or but lightly marked with black; in supralabials, suffused with dusky coloring and often bearing elongate black markings which lack the characteristic wedge shape of black markings on pale supralabials of *elegans;* in predominantly olive coloring of top of head, often with paired yellow markings on posterior part of frontal and on posterior parts of prefrontals, whereas in *elegans* top of head is black except in rostral region; in checkered pattern of back between dorsal and lateral stripes as opposed to black dorsolateral area in *elegans;* in pale, yellowish brown, almost uniformly colored iris exceeding diameter of pupil in width, as opposed to dark, heavily pigmented iris narrower than diameter of pupil in *elegans;* in narrow, elongate, pointed head, as opposed to broader, shorter, blunter head in *elegans;* in relatively larger eyes; in having internasals narrow anteriorly so that their combined contact with rostral is exceeded by contact of either nasal with rostral, whereas in *elegans* internasals are wider anteriorly so that their combined contact with rostral exceeds contact of either nasal with rostral; in oblique suture separating 6th and 7th supralabials, which slants forward, is convex posteriorly and rounded at its upper end, as opposed to more nearly vertical, straighter suture of *elegans,* which is not rounded at its upper end and is sometimes slightly concave posteriorly; in relatively small posterior supralabials as opposed to conspicuously enlarged and swollen posterior supralabials in *elegans;* in more gastrosteges and urosteges (on the average); often 11 infralabials on one or both sides rather than 10 pairs as in *elegans;* in continuity of "6th" scale row from head back to mid-body, as opposed to usual discontinuity or occasional absence of this row in *elegans.*

Differs from *vagrans* in dark brown or grayish brown ground color as opposed to lighter ground color of *vagrans,* often pale brown; in dull, narrow, grayish dorsal stripe usually confined to anterior part of body, as opposed to wider, more yellowish dorsal stripe of *vagrans,* which is usually continuous for full length of body; in large, square-shaped, dorsolateral spots the corners of which overlap, as opposed to small, rounded, well-separated dorsolateral spots of *vagrans;* in suffusion of infralabials with brownish color and occasional heavy marbling of chin with black (but not in fine dots), as opposed to whitish, usually immaculate chin of *vagrans,* which is occasionally finely punctated with black dots; in predominantly olive-colored top of head, not heavily marked with black, whereas in *vagrans* top of head is pale brown, often heavily marked with black posteriorly; in paleness of lowest postocular and scales behind corner of mouth, contrasting with dark color of scales around them, as opposed to dull-colored side of head offering no such contrasting pattern in *vagrans;* in pale, yellowish brown, almost uniformly colored iris as opposed to dark, heavily pigmented iris of *vagrans* which has pale, narrow, yellowish rim encircling pupil; in small pupil, its diameter exceeded by width of iris, as opposed to large pupil of *vagrans,* with diameter exceeding width of iris. Differences in scutellation between *couchii* and *elegans* listed above will also serve to separate *couchii* from *vagrans* except that in numbers of gastrosteges and urosteges and in extent of "6th" scale row *couchii* and *vagrans* agree closely.

Differs from *hydrophila* in usually more reduced dorsal stripe (certain populations of *hydrophila* have a well-developed dorsal stripe); in well-developed lateral stripes, whereas in certain populations of *hydrophila* lateral stripes are faint or absent; in paleness of lower postoculars and areas behind corners of mouth, which contrast with darker colors around them, as opposed to more uniformly colored side of head in *hydrophila;* in brownish infralabials and brownish edges of gastrosteges and occasional marbling with black of entire ventral surface, as opposed to whitish infralabials and immaculate or but slightly marked ventral surface in *hydrophila;* in frequent elongation of black marks on supralabials into rounded blotches, departing from the form of the slender, vertical wedge marks present in *hydrophila;* in often having 11 infralabials on one or both sides (especially in typical individuals from northern part of range) as opposed to 10 pairs of infralabials in *hydrophila;* in having "6th" scale row continuous from head back to mid-body, whereas in *hydrophila* "6th" row is reduced, or is absent, leaving total of 19 rows; in averaging more than 175 gastrosteges in males and more than 170 in females, as opposed to average of fewer than 170 gastrosteges in males and fewer than 164 in females in *hydrophila;* in more urosteges on the average; in pale, yellowish brown iris as opposed to darker, grayish or hazel iris of *hydrophila.*

Comparisons of *couchii* with *gigas* and *hammondii* are made in the discussions of those forms.

Remarks on nomenclature and systematics.—This form was described by Kennicott from a single specimen collected by an expedition of the Pacific Railroad Survey in 1855. The type locality designated was merely "Banks of Pit River, California," but it is evident from the itinerary of the party (Abbott; 1857:56–64) that it did not touch the lower course of the river (below Hatchet Creek).

Kennicott (1859:10), in his original description of this form, and Cope (1900:1043) were both impressed by the elongate appearance of the head, the pointed muzzle, and the heavy black ventral pigmentation shown by the type specimen and characteristic of the population of the upper Pit River.

Ruthven (1908:138) synonymized *couchii* with *Thamnophis ordinoides elegans,* and it was not again recognized as a distinct race until Van Denburgh and Slevin resurrected the name in their revision of western garter snakes (1918:251) and applied it to those of the San Joaquin Valley and southern Sierra Nevada, which they diagnosed as intermediate in characters between *vagrans* and *hammondii.* They stated that *couchii* could be distinguished from *hammondii* by its dorsal stripe, present at least on the neck, by more numerous gastrosteges, frequently 11 rather than 10 infralabials, and less frequently divided preoculars. They regarded certain San Joaquin Valley specimens as intergrades between *couchii* and *hammondii.*

In explaining the differences between *couchii* and *vagrans* Van Denburgh and Slevin (1918:255) concluded: "Intergradation between *T. o. couchii* and *T. o. vagrans* is to be looked for in western Nevada." In discussing the close relationship of *couchii* to *elegans* they stated that *elegans* is confined to the high mountains and *couchii* to the lower levels, but that their ranges meet, and " . . . specimens showing intermediate characters are found at the points where *T. o. couchii* and *T. o. elegans* come in contact as at Jackass Meadows, 7,750 feet, Tulare County, and in Yosemite Valley. At other places, as at Fallen Leaf Lake, El Dorado County, and at Glenbrook, Nevada, snakes of both types have been taken but no intermediate specimens have been secured."

The present study has shown that neither the hypothetical *couchii-vagrans* intergrades nor the supposed *couchii-elegans* intergrades actually exist as such. *T. o. couchii* and *vagrans* meet in western Nevada and in the Sierra Nevada without any merging of their subspecific characters, and *couchii* and *elegans* have been collected together at many localities. The specimens listed as intergrades between them by Van Denburgh and Slevin are either *vagrans* (Jackass Meadows) or are typical of *elegans* (Kings River; Yosemite Valley) or *couchii* (Yosemite Valley); none is intermediate.

Stejneger (1893:212), writing of *"Thamnophis hammondii"* (= *T. o. couchii*), observed: "Its range overlaps to a great extent that of *Th. vagrans* without affecting the purity of the type, and as both are found in the identical localities, as well proved by the present collection, there seems no valid reason for regarding them as subspecies of the same species." On the Death Valley Expedition, both *couchii* and *vagrans,* as now understood by me, were collected in the Owens Valley and along the upper Kern River.

In resurrecting the name *couchii,* Van Denburgh and Slevin applied it chiefly to snakes of the southern Sierra Nevada and the San Joaquin Valley, and no material was available to them from the region of the type locality.

In 1934 I visited the upper Pit River and obtained a single specimen of *couchii* at Hat Creek near its mouth; another was seen at this same locality. In 1935 I collected a series a few miles farther down the Pit River, at Britton Reservoir. Although differing strikingly from *couchii* collected in other parts of the range, all agree closely with the type specimen, as described by Kennicott and Cope, in having elongate, pointed heads and heavy black markings on the ventral surfaces. Undoubtedly the type came from this general region, since the expedition which obtained it explored this part of the Pit River.

Cope's statement (1900:1043) that the type "resembles *vagrans* more than usual" is apparently based entirely on the nature of the pigmentation of the gastrosteges. It is clear that, in spite of this resemblance and their geographically intermediate position, snakes from the Pit River cannot be considered as intergrades between *couchii* of other regions and *vagrans* of western Nevada. Rather, they represent a highly differentiated population, even more distinct from *vagrans* in facial markings, eye color, shape of head and of head scales, and number of infralabials than are other populations of *couchii.* Furthermore, their range does not extend across the plateau region of northeastern California, but is restricted to swift rocky streams and gorges where the Pit River Gap cuts through the Sierra Nevada mountain chain—probably entirely west of Modoc and Lassen counties. In this part of northeastern California a gap of a hundred miles or more exists between the ranges of *couchii* and *vagrans;* where they meet at Pyramid Lake and farther south, they overlap without intergrading.

Although series from the southern Sierra Nevada, from the Owens Valley and other parts of the range, differ markedly from typical *couchii,* these populations do not display peculiar distinctive characters, but are in varying degrees intermediate between *couchii* and *gigas* or *couchii* and *hydrophila.* They have therefore been included with *couchii,* though its subspecific characters are strongly developed only within a relatively small area which happens to coincide with the region of the type locality.

Geographic variation and intergradation.—Specimens from the northern end of the range of *couchii* from the Pit and Feather rivers have more gastrosteges and urosteges than have those from other parts of the range. All the Pit River specimens have 11 infralabials on both sides, except one specimen which has the number reduced to 10 on one side. In the specimens from the Feather River 11 is the most frequent number of infralabials but many snakes show a reduction to 10 on one or both sides. In series from more southern parts of the range, 10 is the more usual number of infralabials, but often there are 11 on one or both sides.

In snakes from Britton Reservoir region of the Pit River, the facial markings are peculiar. The wedge marks usually present in this and other subspecies along the posterior borders of the supralabials lack the usual slender, pointed shape. They are of rounded outline and elongated, not extending downward to edge of mouth but overlapping posteriorly onto the anterior portion of the scale behind, and likewise prolonged anteriorly. In some of the specimens examined, marks on successive labials, especially those of the 4th and 5th, actually meet and fuse, tending to form a longitudinal bar. The two lower postoculars are of a pale color, and this light area is continuous posteriorly across at least the lower anterior corner of the anterior temporal and the upper edges of the two posterior supralabials to the anterior end of the lateral stripe; behind them a black "postoral crescent" extends ventrally to the level of the infralabials, thus cutting into the lateral stripe. The dorsal stripe is dull, tan colored, but distinct for the full length of the body. The infralabials are dull with brownish suffusion, especially the posterior ones; the chin is usually marbled with black, heavily in some of the specimens. The gastrosteges are blotched and marbled with black, some so much so that black is the predominating color of the ventral surface. Parietal spots are bright yellow and well developed. Yellowish markings are present on top of the head on the posterior portions of the frontal and the prefrontals.

Specimens from Tehama and Shasta counties, California, taken in the foothills east of the Sacramento River, show affinity to those of the Pit River but differ from them as follows: Gastrosteges fewer, average size larger, facial markings less characteristically developed and with less contrast between dark and light areas, less black on chin and ventral surface, number of infralabials occasionally reduced to 10. In a specimen from the Sacramento River near Red Bluff (Mus. Vert. Zoöl. No. 9925) the "6th" scale row is much reduced and extends less than 30 per cent of the distance from head to anus, and the infralabials are reduced to 10 on both sides. The chin in this specimen is slightly marbled with black. Specimens from the upper Sacramento River from Shotgun Creek and 7 miles south of Dunsmuir are definitely *hydrophila,* as are those from Cottonwood Creek, Tehama County, and from eastern Trinity County at Deerlick Springs, and from 10 miles south of Trinity Center; all have distinct dorsal stripes, "6th" scale row reduced or absent, number of gastrosteges much reduced, coloration more gray toned, no contrasting facial markings, no yellow on top of head, only 10 infralabials on each side, and preoculars undivided.

Specimens from the middle fork of the Feather River are in nearly all respects intermediate between those of the Britton Reservoir region and those of the southern Sierra Nevada. In them, black markings on the ventral surface are much reduced, often entirely absent on the chin. Supralabial wedge marks are in most specimens typically developed, slender, confined to the posterior portion of each scale, and not elongated longitudinally. Infralabials are nearly white with but little brownish suffusion except on the three posterior ones. Gastrosteges and urosteges average fewer than in the series from the Pit River, and the infralabials are frequently 10, rather than 11, on one or both sides. Two individuals are melanistic and are mainly black in color both above and below. A few of the 38 specimens are heavily marbled with black on the chin and gastrosteges; the majority are pale ventrally, with only a faint speckling of black medially on the ventral surface.

Specimens from Susan River also approach typical *couchii* in characters. In one juvenile (Mus. Vert. Zoöl. No. 17484) the chin is nearly all black, and the ventral surface is continuously black medially from the head to the distal portion of the tail. Other specimens from the same locality have but little black on the ventral surface, and the supralabial wedge marks are slender as in specimens from the Sierra Nevada. The gastrosteges and urosteges are reduced in number and the infralabials are 10 rather than 11.

In specimens from the American River the dorsal stripe is reduced and is present only on the neck; the supralabial wedge marks are slender, the supralabials are dull, brownish in color, and there is no contrasting facial pattern. The postoculars and the scales at the angle of the jaw are brownish and but little paler than those around them. The infralabials have a dusky suffusion. The gastrosteges are dusky along their edges but have little black pigmentation ventrally. The lateral stripe is pale brown, but distinct from the dark dorsal coloration. This description holds, in general, for other specimens from the west side of the Sierra Nevada as represented by series from Yosemite Valley, and from the Merced River, Kings River, and Kern River. In these specimens the dorsal stripe is reduced and not distinct except on the neck, the ventral surface is but little spotted or marbled with black, and the chin is usually immaculate, the supralabials are usually dusky with slender wedge marks, the lateral stripe is brownish, contrasting facial markings are but little developed; the preocular is usually undivided, the gastrosteges and urosteges are fewer than in typical *couchii*, the infralabials are 10 rather than 11.

In specimens from the Truckee River the labials are pale with but little brown coloring and the ventral surface is but little marked with black. In number of gastrosteges, urosteges, and infralabials these snakes closely approximate specimens from the Sierra Nevada.

One from the Carson River (Mus. Vert. Zoöl. No. 18736) is heavily pigmented ventrally; several others have the gastrosteges merely dotted medially. Specimens from near the edge of the San Joaquin Valley, from Fresno and Greenhorn Mountain, show intergradation with *gigas*.

Although *couchii* and *hammondii* show trends toward each other in certain characters, intergradation is not complete, and their ranges are separated by a barrier, the crest of the Tehachapi Mountains, where no permanent water supply is available.

T. o. couchii is common along the Kern River and several have been collected in the next drainage basin to the south, that of Walker Basin Creek. This is the southernmost locality from which I have examined specimens. Specimens from here, compared with those from more northern localities, tend toward *hammondii* in having parietal spots yellower and more distinct, supralabials pale; yellow of lateral stripe extending dorsally to include scales behind corner of mouth but interrupted in neck region by a black area extending ventrally to within 4 scales of gastrosteges; ventral surface pale, nearly immaculate; eyes relatively large.

However, these specimens are abruptly different from *hammondii,* and resemble *couchii* in having relatively large dorsolateral spots the corners of which overlap, and in having higher numbers of gastrosteges. It is probable that snakes of this type occur also in Caliente Creek and Tehachapi Creek, which lie to the south of Walker Basin Creek and are confluent with it at times when the water supply is abundant. In April, 1936, persons living at Tehachapi Creek told me of seeing these snakes, and a ranger at Castaic Lake said that they were abundant there a few years before; but I failed to find any. At the time of my visit the lake was low, strongly alkaline, barren of any riparian vegetation, and not fed by any running stream. It seems highly improbable that any garter snakes now occur in that region, since apparently there is no permanent water supply north of the Tehachapi Divide in Tejon, El Paso, Tunis, Pastoria, Grapevine, and San Emigdio creeks.

I am informed by Dr. Stejneger that two specimens from Fort Tejon in the National Museum, both catalogued as No. 5496, are cotypes of *hammondii.* One of these, an adult female, has 170 gastrosteges, thus exceeding nearly all females of *hammondii* in numbers of these scales, and the other has 163 and is thus near the minimum for *couchii.* Cope (1900:1042) figures one of these specimens. In his drawings the eyes are relatively small, not protruding beyond the profile of the supralabials as seen from dorsal view, the posterior genials are not conspicuously longer than the anterior ones, and the suture separating the 6th and 7th supralabials is more nearly vertical than in most specimens of *hammondii.* In all these characters it is nearer to *couchii* than to *hammondii.*

Ruthven (1908:136) in his table showing numbers of preoculars in "*hammondii*" (=*hammondii* and *couchii*) indicates 5 specimens from "Tejon, California"; all have undivided preoculars. This is strong evidence that they should be referred to *couchii,* because the preoculars are usually divided on one or both sides in *hammondii.*

The foregoing data on *couchii* at the southern end of its range, considered together with an analysis of variable characters throughout the entire ranges of *couchii* and *hammondii,* lead to the conclusion that although partial intergradation occurs, it is not comparable to the continuous, gradual, and complete transition in characters which takes place between other intergrading forms of *ordinoides.* The relationship between *hammondii* and other members of the *Thamnophis ordinoides* group is therefore best expressed by classifying *hammondii* as a distinct species.

Habits and habitat.—Habitat data are available for 94 individuals. Of this number 54, more than half, were actually in the water, which, for each individual, was that of a flowing stream. These individuals were either in the water when they were found or they dove into it from the stream bank before they could be collected, and some of them permanently escaped the collector. Thirty-two more were collected at the edge of the water. Most of these were collected by the writer and are known to have been found within 5 feet of the water's edge, usually coiled on boulders, rarely on grassy banks, but always in places where the stream bed was rocky. Others placed in this category include specimens taken by Museum of Vertebrate Zoölogy collectors, whose field notes indicate that the snakes were taken in the near vicinity of water though usually the exact distance was not specified. Only 5 of the 94 were collected in situations definitely away from the edge of the water. All these were taken in the general vicinity of streams or rivers, and probably in riparian associations (except one taken "in tall dry grass") but were several or many yards from the water, which was thus not available as a means of instantaneous escape.

At Cromberg, on the middle fork of the Feather River, 1 found *couchii* much more abundant than at any other locality where I collected; in two days 40 were taken, and many others escaped. This was in the Transition Life Zone of the northern Sierra Nevada in a forest of white fir, Douglas fir, incense cedar, and black oak. Environmental factors which seemed to favor the presence of these garter snakes were: the permanently abundant supply of fresh, clear water; the rocky character of the river bottom and shores; the slowly moving current with many shallow, protected pools near the shore; the high water temperature; the abundant shelter in riparian thickets and in grass tussocks on boulders along the bank and in the river; the abundance of small fish (trout and suckers) in shallow water near the edge of the river. Frogs (*Rana boylii*) occurred there also, but not abundantly; more snakes than frogs were seen. Most of the snakes were seen lying submerged in shallow water near the edge of the river, but some were actively swimming or crawling among rocks under water, apparently foraging. When alarmed they made for deep water, if it was possible to do so; otherwise they swam along the bottom and tried to hide among rocks and grass along the bank.

Feeding data, based mainly on preserved material, also on field notes (I. L. Hussey *in litt.* to J. Grinnell), and published literature (Van Denburgh and Slevin, 1918:256), are available concerning 18 snakes of this subspecies, which had eaten a total of 55 animals. One food item was an adult toad (*Bufo boreas*); all others were strictly aquatic animals: 37 fish and 17 tadpoles. Tadpoles (*Bufo boreas, Rana* sp.) had been eaten by only 3; fishes had been eaten by 13.

Of the 37 fish eaten, 32 were tentatively or positively identified as trout. No slugs, worms, salamanders, frogs, lizards, mice, birds, or other terrestrial animals such as are preyed upon by *elegans* and *ordinoides* were found in any of the specimens examined. Snakes which contained food were from seven well-scattered localities representative of the range of this subspecies.

Records of occurrence.—Specimens examined, 162, in the Museum of Vertebrate Zoölogy (unless otherwise indicated), from the following localities:

Nevada. *Washoe County:* (?) Halleck or Pyramid Lake, 1[7][*]; Pyramid Lake, 1[4]; Truckee River at "Camp 12," 1[7]; (?) vicinity of Reno, 1[1]; Verdi, 1. *Churchill County:* Fallon, 1.

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[*] Explanation of references: [1] University of Nevada Zoölogy Department; [2] California Academy of Sciences; [3] University of Michigan Museum of Zoölogy; [4] Natural History Museum, Stanford University; [5] Collection of L. M. Klauber; [6] San Diego Society of Natural History; [7] United States National Museum.

Lyon County: Yerington, 1. *Ormsby County:* near Carson City, 2^4; *Douglas County:* Glenbrook, 1^3.

California. *Lassen County:* Susan River 8 miles west of Susanville, 4. *Shasta County:* Pit River at mouth of Hat Creek, 1, and at Britton Reservoir, 9; Battle Creek at Longs ranch, 1^4; Sacramento River 7 miles east of Anderson, 4. *Tehama County:* Paynes Creek at Elliots, 2, and at Dales, 4; 1 mile northeast of Red Bluff, 1; Red Bluff, 1; Cones 4 miles south of Red Bluff, 3. *Plumas County:* east fork of north fork of Feather River 1 mile west of Virgilia, 1; Cromberg, middle fork of Feather River, 38. *Yuba County:* Strawberry Valley, 1^4. *Nevada County:* Truckee River 2 miles above Floriston, 8. *Placer County:* Loomis, 1; Tahoe, 3^4; Red Point, 1^4. *Eldorado County:* American River at Chili Bar, 1; and 3 miles west of Kyburz, 4400 feet, 2; Fyffe, 1^4; Riverton, 1^2 and 2^4; Fallen Leaf Lake, 3 (2^4, 1^3); Tallac, 1^4; Lake Tahoe, 1^4. *Amador County:* Oleta, 1^5. *Tuolumne County:* Priest Hill, 1^4; Tuolumne Lodge, 1^3. *Mariposa County:* Pleasant Valley, 3; Yosemite Valley, 3; Elevenmile, 1^5; south fork of Merced River, 4^3, Calaveras Big Trees, 1^2; Visalia, 1^5. *Alpine County:* Markleeville, 1; Carson River 2 miles southeast of Markleeville, 5900 feet, 4. *Madera County:* Raymond, 1. *Inyo County:* Bircham Canyon, Owens River at mouth of Rock Creek, 2; Round Valley, 1^6; Owens River near Laws, 1^6; Owens Valley, 1; Laws, 1; Owens River above Aberdeen, 1^3. *Fresno County:* Hume, 1; Fresno, 5^4. *Tulare County:* Trout Creek, 6000 feet, 1; Trout Meadows, 1^4; Kern River near Bodfish, 1; Little Kern River Lake, 1^4; Little Lake, 11; Quaking Aspen Meadows, 1. *Kern County:* Greenhorn Mountain, 6000 feet, 1; south side of Thompson Canyon, Walker Basin, 3900 feet, 2; Walker Basin, 3900 feet, 2; Walker Basin Creek, 1.

Stejneger's records (1893:213) of *Thamnophis hammondii* from Inyo County at Alvord, 10 miles north of Bishop, Cartago, and Lone Pine, and from Kern County at various points on the Kern River almost certainly pertain to the present form.

Thamnophis ordinoides gigas, new subspecies
(Giant Garter Snake)

Eutaenia Hammondii, Cooper, 1870:71

Thamnophis hammondi, Ruthven, 1908:133 (part)

Thamnophis ordinoides couchii, Van Denburgh and Slevin, 1918:251 (part), pl. 12

Type.—Adult female, Mus. Vert. Zoöl. No. 5428, collected at Gadwall, Merced County, California, May 16, 1914, by H. C. Bryant.

Range.—Floor of the Great Valley of California from Sacramento and Antioch south to Buena Vista Lake; confined to vicinity of permanent fresh water (see fig. 11, p. 60).

Diagnosis.—Maximum number of scale rows on anterior part of body usually 23, of which the 5th on each side is of variable length and usually short, 21 rows continuous from head posteriorly well beyond mid-body; supralabials 8, 8; infralabials 10, 10, or occasionally 11 on one or both sides; gastrosteges fewer than 170 in males and fewer than 165 in females; size large (largest form of the genus), with a head and body length in adults often exceeding 700 mm., occasionally exceeding 1000 mm.; ground color dull brown; dorsolateral black spots reduced in size and well separated; head brown with no contrasting facial markings; parietal spots absent or faint; ventral surface brownish; lateral stripe often not developed; head elongate, narrow posteriorly, with pointed muzzle.

Coloration.—Description of freshly killed adult male, Mus. Vert. Zoöl. No. 19358, collected at Dos Palos, Merced County, California.

Top of head Ecru-Olive and Buffy Olive; slightly darker in rostral region than posteriorly; several irregular faint blackish streaks on parietals near mid-line; no parietal spots; supralabials Light Grayish Olive; supralabial wedge marks when present reduced to narrow black lines along posterior edges of scales, absent altogether on five anterior supralabials; iris Deep Olive-Buff; second scale behind corner of mouth mainly black in contrast to paler color of surrounding scales, black area irregularly continuous from this scale posteriorly for a distance about equal to combined lengths of four or five scales, covering only portions of most of scales involved; small black areas on lower portions of temporals; ground color on body Ecru-Olive; dorsal stripe suffused with olive ground color but discernible for full length of body, nearest Reed Yellow anteriorly, duller and less distinct posteriorly, involving medial row and adjacent portion of row on each side; borders ill defined and shading into dorsolateral color; lateral stripes Reed Yellow suffused with Citrine-Drab, especially on lower portion of second scale row and on posterior part of body; dorsolateral spots inconspicuous, mainly confined to skin between scales, from one to one and three-fourths times length of a scale, irregular in outline, mainly confined to ends or edges of several scales, but not extending to their centers; lateral flecks Pale Olive-Buff anteriorly, Tilleul Buff on posterior part of body, inconspicuous and entirely confined to skin between scales; mainly in areas between scales of the six lower rows and between those of the three upper ones, largely absent in areas between scales of 6th and 7th or those of 7th and 8th rows; genials and a few of most anterior gastrosteges Ivory Yellow; most of gastrosteges on anterior half of body Pale Olive-Gray with Deep Olive Gray areas on their lateral portions; posterior gastrosteges Light Olive-Gray medially, Deep Olive-Gray laterally and posteriorly; urosteges mainly Deep Olive-Gray with small areas of Light Olive-Gray.

Comparisons.—As contrasted with typical *couchii, gigas* differs as follows: Larger (head and body length often more than 800 mm.); gastrosteges and urosteges usually fewer; maximum number of scale rows 23, as opposed to 21 in most *couchii;* 10 pairs of infralabials rather than 11; dorsal and lateral stripes less distinct or absent; parietal spots fainter or lacking, whereas often conspicuously developed in *couchii;* dorsolateral body spots smaller and well separated, whereas in *couchii* these spots are larger and closer together so that corners of adjacent spots often overlap, producing checkerboard pattern; side of head dull brown with no contrasting pattern, as results in *couchii* from paler color of scales behind corner of mouth and in postocular region; conspicuous black marks on supralabials lacking (elongate blotches or wedge marks in *couchii*); and extensive black markings on ventral surface lacking, whereas in *couchii* gastrosteges and even chin may be heavily marbled with black.

As contrasted with *hammondii, gigas* differs in the following particulars: Lateral stripe is duller colored and less sharply defined or absent, dorsal stripe is present (though faint) for much of its length, whereas stripe in *hammondi* is restricted to neck region and never more than a few scales long; supralabials dull brown and lacking distinct wedge marks, whereas in *hammondii* supralabials are pale on their lower portions and have slender, black, sharply defined wedge marks; ventral surface darker, dull brownish as opposed to nearly white; eye smaller and not protruding beyond profile of supralabials as seen in dorsal view; suture between 6th and 7th supralabials more nearly vertical rather than oblique, and if projected passing behind rather than across the eye; preocular single on each side of head rather than usually divided.

Remarks on nomenclature and systematics.—*T. o. gigas* was not recognized as distinct from *couchii* by Van Denburgh and Slevin (1918), who had no typical material of the latter form. Their discussion of *couchii* was based mainly upon specimens of *gigas,* and upon intermediate specimens (herein referred to *couchii*) from the southern Sierra Nevada.

My comparisons of series of typical *couchii* with series from the San Joaquin Valley has led to recognition that the latter belong to a distinct form since they are strikingly different in characters. However, the relationship between *couchii* and *gigas* is close, as shown by the gradual transition in characters between them, in contrast to the abrupt transition in characters which takes place, for example, between *couchii* and *hydrophila. T. o. gigas* may be regarded as a recent derivative of *couchii,* which has differentiated in response to the special set of environmental conditions obtaining on the floor of the Great Valley of California.

Geographic variation and intergradation.—The population of *gigas* in the

Buena Vista Lake basin is at present isolated from populations of the San Joaquin Valley. Although actual isolation of northern and southern populations of *gigas* has occurred only recently, since the settling of the San Joaquin Valley, it was preceded by differentiation in extent of the 5th scale row. On the average this row is more than twice as long in the Buena Vista Lake snakes (see p. 86). In each of the five available specimens from Buena Vista Lake, as well as in live individuals seen by me in that general region but not collected, a dorsal stripe was present. In some of those from more northern localities both dorsal and lateral stripes are almost obliterated, and the pattern is a monotone brown. Van Denburgh stated (1922:843): "The largest specimens sometimes show no lateral lines or other markings." However, this lack of markings is not peculiar to large individuals, since it is shown by the two smaller specimens examined by me: Mus. Vert Zoöl. No. 6833 from near Mendota, Fresno County (length to anus 495 mm.), and Cal. Acad. Sci. No. 13636 from Los Banos, Merced County (length to anus 261 mm.).

One from Antioch Bridge, Sacramento County, has a dorsal stripe which is paler and more distinct than that in any of the other specimens examined. This locality is only a few miles east of the known eastward limit of *atratus,* which has been collected at Mount Diablo and Walnut Creek in Contra Costa County. It is possible that the ranges of the two forms meet, or did so formerly, but there is no indication that intergradation occurs. It could hardly be expected in forms so different in ecologic preferences and structural characters.

Specimens from Fresno (Stanford Mus. Nat. Hist. Nos. 1753–1756 and 4127) are like typical *gigas* in coloration but have more gastrosteges and urosteges, and none has more than 21 scale rows on the body. Though they have been listed under *couchii,* they may be considered intergrades, and perhaps their relationship is closer to *gigas* than to typical *couchii.* All other specimens of *couchii* from near the edge of the San Joaquin Valley, including those from Oleta, Amador County, Raymond, Madera County, Visalia, Tulare County, and those from the lower Kern River, Kern County, approach *gigas* in coloration in having the side of the head dull colored with no contrasting facial pattern, dorsal and lateral stripes obscure, and ventral surface and infralabials brownish.

Habits and habitat.—Van Denburgh's account (1922:791) of this form at Buena Vista Lake suggests that it is aquatic in habits; he mentions finding colonies of these snakes in tule patches at a distance from shore, and he was impressed by their shyness.

Richard Hunt (MS) recorded that a specimen of *gigas* collected by him (Mus. Vert. Zoöl. No. 6833) near Mendota, Fresno County, June 18, 1918, was found swimming in the middle of a slough at 7 P.M. when he was crossing the slough in a boat.

On April 10, 1936, I hunted these snakes along irrigation canals between Buttonwillow and Tupman, Kern County (see pl. 3, fig. 3). Although they were fairly common, catching them by the usual method of stealthily approaching and seizing them by hand proved to be an impossibility, partly because of the habitat conditions under which the snakes were found, but chiefly because of their alertness and timidity. The canals where the snakes were seen were usually about 15 feet wide, with nearly vertical banks and with a current of slightly turbid water several feet deep. The banks were usually overgrown with tules, willows, and weeds, making it difficult to find the snakes. The first one seen was probably well over 4 feet in length. It was basking in a clump of dead brush over the water, but it took instant alarm upon sighting me about 30 feet distant, and plunged into the canal with a loud splash. While I was waiting for it to reappear, a smaller one emerged at the surface in the middle of the canal. For several seconds it swam with slow undulations, maintaining its position in the current, then turned in toward the bank on which I was standing. Before reaching this destination it seemed to notice me, although I was standing motionless several feet above the water. It checked its movement, hesitated, and then struck out toward midstream, dove, and disappeared. Later it reappeared at the opposite bank and crawled over sticks lying in the water, but it still showed signs of uneasiness and dove again after a few seconds. Six others were seen swimming in the canal or were glimpsed as they dove into it from weeds or bushes over the edge of the water. Two were found crushed on the pavement where roads crossed canals.

When I returned to this same locality on April 14, three snakes were found, probably the same individuals seen on the previous occasion. The visit was made late in the afternoon and the snakes were relatively sluggish though still difficult to approach; all had fed earlier in the day, as was shown by swellings in their contours.

Of specimens examined by me only one contained food; Calif. Acad. Sci. No. 36071, collected at Los Banos, June 28, 1912, had eaten a fish which was too well digested to be identified.

Wherever these snakes were seen by me, bullfrogs and carp were extremely abundant, and were by far the most conspicuous animals of the aquatic fauna. It seems probable that at present these two introduced species figure importantly in the food of *gigas*.

Within the range of *gigas*, those kinds of aquatic animals which constitute most of the food of *hydrophila* and *couchii* are mostly absent. Trout, *Cottus*, *Rana boylii*, *Dicamptodon*, and *Triturus* do not occur in streams on the floor of the San Joaquin Valley, and *Hyla regilla* and *Rana aurora draytonii* are not common there. It seems evident that *gigas* must differ markedly from *hydrophila* and *couchii* in its foraging habits, for those subspecies catch their active prey beneath rocks on the stream bottom, whereas *gigas* is confined to streams having mud bottoms.

The wariness of these snakes is probably correlated with their open habitat. Water is usually shallow in this habitat; rocks and logs that might serve as shelter are absent both under water and along the shores; trees and bushes are absent along the edge of the water, and the snakes are not screened from view from above. Under these conditions they are in constant danger from herons, marsh hawks, and other predatory birds which might drop down upon them or seek them out in the shallow water. Alertness and wariness are perhaps more necessary to them than to snakes in upland habitats, which often are screened from view by overhanging vegetation, and which have tangles of brush, driftwood, boulders, and deep pools immediately available for shelter.

The limited data available regarding the habits of this subspecies indicate that it is more aquatic than any of the other forms studied. Individuals seen in the water swam and dove with great facility, but none was seen away from the water; elsewhere desert conditions prevailed. In the region where it occurs, soil temperatures are often so high that surface foraging would be impossible for a strictly diurnal snake; thus the aquatic niche is the only one open to snakes of this species. No member of the Elegans group within the species occurs within the geographic range of *gigas*.

Records of occurrence.—Specimens examined, 21, all from California, in the California Academy of Sciences (unless otherwise indicated). *Sacramento County:* Sacramento River at west end of Antioch Brigdge, 1 (Univ. Mich. Mus. Zoöl.); 10 miles south of Sacramento, 1 (Sacramento Junior College). *San Joaquin County:* Mormon Island, 1 (Sacramento Junior College). *Merced County:* Los Banos, 6; Merced, 1; near Dos Palos, 2 (Mus. Vert. Zoöl.); Gadwall, 2 (Mus. Vert. Zoöl., 1). *Fresno County:* San Joaquin River 1½ miles north of Mendota, 1 (Mus. Vert. Zoöl). *Kern County:* Buena Vista Lake, 5; near Buttonwillow, 1 (Mus. Vert. Zoöl.).

Thamnophis hammondii (Kennicott)

(California Garter Snake; Water Snake; Hammond Garter Snake)

Eutainia Hammondii Kennicott, 1860*b*:332 (original description)
Eutaenia Couchii, Cooper, 1870:64
Eutaenia hammondii, Yarrow and Henshaw, 1878:1637 (part)
Eutaenia marciana, Yarrow and Henshaw, 1878:1638
Eutaenia elegans couchii, Cope, 1892:656 (part)
Tropidonotus vagrans, Boulenger, 1893:202 (part)
Thamnophis hammondii, Van Denburgh, 1897:212 (part)
Thamnophis ordinoides hammondii, Grinnell and Camp, 1917:181 (part)
Thamnophis ordinoides hammondi, Stephens, 1921:63

Type.—Male, U. S. Nat. Mus. No. 894; collected at San Diego, California, by W. A. Hammond.

Range.—Coastal slope west of summit of Coast Range divide, from Monterey Bay, California, through Sierra San Pedro Mártir in northern Lower California. Confined to near vicinity of permanent fresh water (see fig. 12).

Diagnosis.—Maximum number of scale rows on anterior part of body ordinarily 21 (rarely 23), the 5th (when 21 are present) continuous from head back to mid-body; supralabials 8, 8; infralabials 10, 10; preocular on each side usually divided into two plates by horizontal suture; dorsal stripe confined to neck region; usually faint, sometimes altogether absent; lateral stripes distinct, yellowish; dorsal ground color brown or gray; two rows of alternately placed black spots on each side between middorsal line and lateral stripe, each spot small and of irregular outline, well separated from adjacent spots; supralabials pale, dusky above, marked posteriorly with slender, sharply defined wedge marks which extend downward to edge of mouth; top of head brown, with conspicuous bright yellow parietal spots margined with black; yellow of lateral stripe extended dorsally to last supralabial, but interrupted by black markings which extend downward in neck region; ventral surface pinkish, immaculate or but little marked with black; posterior supralabials relatively small, suture separating 6th and 7th slants obliquely forward, usually in plane intersecting eye; eye relatively large, often protruding conspicuously beyond profile of supralabials as seen in dorsal view; iris pale, yellowish brown, uniformly colored or nearly so; pupil small, its diameter conspicuously exceeded by width of iris; gastrosteges average less than 170 in males and more than 159 in females; chin white, but with narrow black margins along most of sutures separating infralabials; muzzle pointed; contact of either nasal with rostral exceeds combined contacts of both internasals with rostral; posterior genials conspicuously longer than anterior genials.

Coloration.—Description of living adult female, Mus. Vert. Zoöl. No. 19360, collected near Hernandez, San Benito County, California:

Top of head uniformly Deep Grayish Olive except for parietal spots, which are Martius Yellow slightly suffused with dusky ground color, in contact along mid-line, slightly longer than wide, and surrounded by a black area about equal to their own transverse diameters. Supralabials mainly Grayish Olive with slender black wedge marks along their posterior edges which extend downward nearly or quite to edge of mouth; lower portions of 4th, 5th, and 6th supralabials paler, nearly white, contrasting with dusky coloring of upper portions and tinted with Pale Pinkish Buff; lower and middle postoculars Grayish Olive, skin between them tinted with yellowish contrasting with darker coloring of other scales; skin beneath lower preocular separating it from supralabials yellowish; loreal edged with black superiorly; rostral, nasals, loreals, and preoculars mainly Grayish Olive; iris Dark Olive-Buff; a black mark behind head beginning one scale behind and two scales above corner of mouth, two scales wide and three scales long,

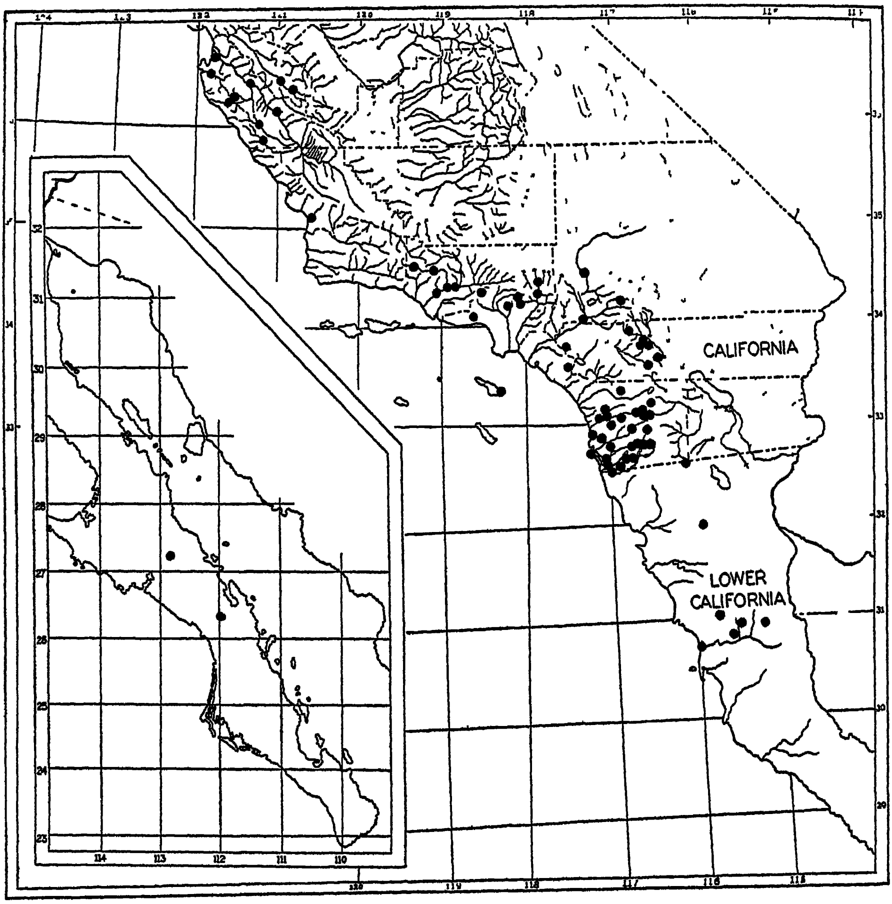

Fig. 12. Range of *Thamnophis hammondii* (dots indicate localities of specimens examined) in southwestern California and northwestern Lower California, and (inset) range of *Thamnophis digueti* in central Lower California.

forming enlarged first spot of series in dorsolateral region, which are arranged in two alternating rows on each side; spots mainly confined to 4th and 8th scale rows on each side; each spot occupies an area of less than half that of a single scale, being confined mainly to anterior portion of a single scale; skin between scales on body mainly black; pale lateral flecks on body Light Lumiere Green, not showing unless skin is stretched; dorsal ground color Deep Grayish Olive, most of the scales finely dotted with black on their anterior portions and with keels paler, Grayish Olive; lateral stripe Pale Orange Yellow at anterior end, slightly suffused with dusky ground color posteriorly, but well defined for full length of body on 2d and 3d scale rows above gastrosteges, middorsal region of neck paler than general ground color, Grayish Olive with yellowish skin between scales, showing trace of dorsal stripe; chin mainly white with black posterior edges along all of infralabials; mental plate, 1st and 2d infralabials, and posterior portions of 3d, 4th, 5th, 6th, and 7th infralabials and most of 8th, 9th, and 10th buffy colored; first 5 gastrosteges white except for faint ochraceous tinge at outer margins; other gastrosteges tinted with Pale Ochraceous Salmon; posterior gastrosteges mainly Pale Olive Gray or Pale Smoke Gray tinted with ochraceous, darker especially along posterior edges and tinted with Pinkish Cinnamon; gastrosteges edged with black anteriorly, this narrow black region widening to form a spot on anterolateral corner of each gastrostege; black areas mainly hidden by overlapping of scales; corners of gastrosteges darker, Light Neutral Gray; lower portion of 1st scale row Light Neutral Gray.

Comparisons.—*T. hammondii* shares parts of its range with *atratus*, *elegans*, and *hueyi*; it tends to intergrade with *couchii*, and obviously its closest relationship is with the isolated species *digueti*. Comparisons with all these forms are made; comparison with *digueti* is in *atratus*.

T. hammondii, as compared with *atratus*, differs in having: no dorsal stripe or only trace of one in neck region, whereas *atratus* has bright dorsal stripe for the full length of body and tail; pale gray or brownish gray color, as opposed to dark, nearly black, slaty gray, or (in northern coastal region) sometimes reddish brown ground color of *atratus*; no red markings such as are often present on dorsolateral area, lateral stripe, or ventral surface of body and tail in *atratus*; no bright yellow in ventral coloration, as opposed to bright yellow chin and yellow blotches on gastrosteges often present in *atratus*; pale yellowish brown iris, as opposed to gray (sometimes greenish) or (in northern part of its range) heavily pigmented iris of *atratus*; preoculars double, as opposed to single; 21 scale rows continuous back to mid-body as opposed to 19 scale rows for part or all of this distance under the discussion of that species.

Differs from *elegans* in having: no dorsal stripe, as contrasted with well-developed bright yellow stripe of *elegans*; ground color pale rather than black or very dark brown; supralabial wedge marks more attenuate, slender, extending downward to edge of mouth, as opposed to blunter, less attenuate, wedge marks of *elegans*, which do not ordinarily reach edge of mouth; iris pale, yellowish brown, uniformly colored, as opposed to the heavily and unevenly pigmented iris of *elegans*; 21 scale rows present from head back to mid-body, whereas 5th row of *elegans* is usually shortened, leaving only 19 rows for part of this distance; posterior genials conspicuously longer than anterior, as opposed to subequal genials of *elegans*; eye relatively large entering profile as seen in dorsal view, as opposed to small eye of *elegans*, which does not enter profile; suture separating 6th and 7th supralabials slants obliquely forward so that it usually intersects eye if projected, as opposed to nearly vertical suture of *elegans*; sutures separating infralabials bordered with black, whereas in *elegans* such marks are lacking and chin is uniformly white.

These differences will serve also to separate *hueyi* from *hammondii* since *hueyi* and *elegans* are similar in most respects.

Differs from *couchii* in having: only 10 infralabials, whereas *couchii* typically has 11 (though throughout much of its range 10 is the more usual number); dorsal stripe entirely absent, or present only on neck, whereas in *couchii* it is usually present for a greater distance along anterior part of body and may be distinct for full length of body; side of head dull colored, with no contrasting facial pattern, whereas in *couchii* preocular and lower postoculars are conspicuously paler than surrounding areas; supralabials pale, especially on their lower portions, with slender vertically attenuate wedge marks posteriorly, whereas in typical *couchii* they may be dusky colored with black markings not closely confined to posterior borders, not forming typical wedge marks, but tending to form elongate blotches; dorsolateral body spots small and well separated, as opposed to the larger spots of *couchii* in which corners may overlap adjacent corners of neighboring spots; chin immaculate, no conspicuous black markings on ventral surface, whereas in *couchii* ventral surface of body and even chin may be heavily marbled with black; eye conspicuously larger; suture separating 6th and 7th supralabials slanting obliquely forward so that it usually passes across eye if projected, as opposed to more nearly vertical suture of *couchii,* which usually passes behind eye if projected.

Remarks on nomenclature and systematics.—In the original description of *hammondii,* Kennicott (1860*b* :332) indicated some of its most distinctive characters, but Cope synonymized it under the name *couchii.* Van Denburgh (1897 :212) recognized it as a distinct species, but also included *couchii* from Kern and Inyo counties, referring other populations of *couchii* to "*Thamnophis vagrans.*" Ruthven (1908 :133) classed *hammondii* as a distinct species, but attempted to show its affinity to *T. angustirostris* and *T. o. elegans.* Specimens here referred to *couchii* he considered to be transitional between typical *hammondii* and *elegans,* and he implied that intergradation might occur between these two forms. He wrote of *hammondii:* "Its resemblance to *angustirostris* decreases in the northern part of its range and *hammondii* comes to resemble another form (*elegans*) which replaces it to the northward. Its resemblance to this form is so close that specimens from near the range of the latter (Inyo, Kern, Tulare, Fresno counties, California) are distinguished with the utmost difficulty. This is brought about by the fact that *hammondii* usually has a single preocular in the northern part of its range and occasionally a dorsal stripe, and it can with certainty be distinguished from *elegans* only when it has two preoculars and no dorsal stripe. However sufficient proof that these forms actually intergrade is wanting."

Grinnell (1908 :166–167) found both *elegans* and *hammondii* at the same general localities along the upper Santa Ana River in the San Bernardino Mountains.

Van Denburgh and Slevin had material of both *elegans* and *hammondii* from the same general regions in southern California and recognized the fact that overlapping occurs between these two forms. They remarked (1918 :239): "Those [*elegans*] from the San Bernardino Mountains also show no departure from this type [typical *elegans*] although their range is in part overlapped by *T. o. hammondii.* No one could question the validity of this race as it occurs in these southern mountains, and the fact that intergrades occur in the more northern portion of its range should not cause us to refuse it recognition."

In treating of the same problem under their discussion of *T. o. hammondii,* they commented (1918 :260): "In the San Bernardino Mountains *T. o. hammondii* occurs with *T. o. elegans* at altitudes of 5000 to 7000 feet. Here the two forms seem to remain true to type, for no intermediate specimens have been taken. *T. o. elegans* seems to be a mountain form while *T. o. hammondii* occupies the lower country as well as the higher elevations."

Grinnell and Camp (1917:179–181) classified the three California forms of this group recognized by them (*ordinoides, elegans,* and *hammondii*) as subspecies of *ordinoides.* In their discussion of *elegans* (1917:180), they remarked: "Thought to intergrade along western edge of its range with *hammondii.*" They disregarded earlier records and specimens of *elegans* from the San Bernardino Mountains within the range of *hammondii.*

Geographic variation and intergradation.—Although *T. hammondii* is a wide-ranging form, it shows but little variation in color pattern. Specimens from Monterey County are least typical. Of the 10 examined, all but one (Mus. Vert. Zoöl. No. 7246, from near San Lucas) have the lateral stripes and parietal spots extremely faint or entirely absent. In two (from Nacimiento River and Church Creek) the dorsolateral spots are larger than in typical *hammondii.* The three from San Benito County are typical in coloration, having distinct lateral stripes and parietal spots, and small dorsolateral black spots on the body.

A specimen from Avalon, Catalina Island (Calif. Acad. Sci. No. 63080) has the following atypical coloration: entire dorsal surface Buffy Brown; black spots on body reduced in size, hardly noticeable except at anterior end of body, confined to edges of scales and skin between them; no trace of dorsal stripe; yellow parietal spots present but small and faint with no black margins; no distinct black markings behind head; sides of neck brown with no conspicuous upward extension of pale ventral color behind corner of mouth; supralabials dusky posteriorly but with no distinct wedge marks, and only slightly paler on their lower portions; no distinct black marks between infralabials though edges of scales along sutures are dusky colored; no distinct lateral stripe on 2d and 3d scale rows; brown dorsal surface passes uninterruptedly into dull-colored ventral surface; gastrosteges mainly Dark Olive-Buff with small light areas in their central portions; anterior gastrosteges lighter. This specimen resembles *digueti* in coloration.

It seems improbable that an endemic population of garter snakes exists on Santa Catalina Island, and the specimen described above may be an abnormally marked individual brought there from the mainland through human agency.

T. hammondii shows definite geographic trends in certain scale characters. The maximum numbers of gastrosteges and urosteges occur in specimens from Ventura County and northern Los Angeles County, where its range is adjacent to that of *couchii;* there is a decrease in numbers of these scales to the southward, most pronounced in specimens from the southern end of the range in Lower California, and in the northern part of the range in Monterey, San Benito, Santa Barbara, and San Luis Obispo counties. It is significant that the populations having the lowest scale counts are geographically nearest to *gigas* and *digueti,* which have fewer gastrosteges and urosteges than *hammondii,* and that the populations having the highest counts of these scales are geographically nearest to *couchii,* which markedly exceeds *hammondii* in numbers of gastrosteges and urosteges.

Apparently the preocular scales are most frequently divided in snakes from the southern part of the range in Lower California—again showing possible affinity to the more southern species *digueti*. Preoculars are most often undivided in series from the San Bernardino and San Jacinto mountains.

The relative lengths of anterior and posterior genials are fairly constant in different parts of the range and the posterior genials are relatively long as compared with those of other races.

As compared with other races of the group which have comparably extensive ranges, *hammondii* shows striking uniformity in all its characters throughout the region of its occurrence. Though geographic variation and apparent tendencies toward other forms can be shown with the large series available, variation within the race is slight as compared with the gaps existing between it and other forms.

Habits and habitat.—Grinnell and Grinnell (1907:49–50) and Grinnell (1908:167) described the aquatic habits of this species in the Los Angeles and San Bernardino Mountains region. Klauber (1924:16; 1934:20) wrote of *hammondii* in San Diego County that it was plentiful along the margins of streams, reservoirs, and ponds. Linsdale (1932:381) wrote: "The following places of capture of this garter snake indicate its choice of habitat in Lower California: among damp grass in marshy ground; curled in a bare spot near creek; under willows near creek; at edge of creek under willow bush; among damp grass at edge of stream; at water's edge among loose rocks and sand; in "spear grass" near marsh; on ground under mesquite tree [=*digueti*, see p. 82]."

Of specimens in the Museum of Vertebrate Zoölogy for which habitat data are available, one was found "in willow sprouts near water," one was "caught on dry river bottom" (of Salinas River), and one was found swimming among submerged rocks in the San Benito River.

Messrs. D. H. Johnson and F. G. Palmer told me of seeing many of these snakes along streams in San Benito County in the summer of 1936, but only two were collected by them. Most of those seen escaped by diving into deep pools where they hid in inaccessible places, often beneath willow thickets. Mr. Jack von Bloeker, Jr., described similar escape reactions in numerous individuals seen by him in a similar habitat in Monterey County in the summers of 1936 and 1937.

T. hammondii is apparently restricted in local distribution to the near vicinity of permanent fresh water and tends to be aquatic in habits. It is most common along streams having rocky beds and bordered by thickets of willow and other vegetation affording shelter. Some of the streams where it occurs become almost dry in summer and are reduced to series of stagnant, disconnected pools. Within the range of *hammondii* watercourses are in general smaller, and less permanent than those in the ranges of *hydrophila*, *couchii*, or *gigas*. Apparently *hammondii* is less aquatic than these forms, at least if Klauber's statement that it is "not uncommon in dryer situations" is correct. However, it probably depends mainly on the water as a place of refuge from danger.

General statements made by authors regarding the food used by *hammondii* include the following items: tadpoles, small frogs and fish (Grinnell and Grinnell, 1907:50); tadpoles, frogs, and fish (Van Denburgh and Slevin, 1918: 260); amphibians and fish (Klauber, 1934:20); insects, tadpoles, and small fish (Stephens, 1921:63). Klauber (1924:16) wrote that a newly captured individual ate 30 *Hyla regilla* in rapid succession.

To summarize available feeding data, based mainly on stomach examinations made by me on specimens, but also including several items recorded by Klauber (1931:72): of 27 snakes, 14 had eaten tadpoles, 10 had eaten metamorphosed tree toads, 3 had eaten fish, 1 had eaten a toad, 1 had eaten an earthworm, and 1 had eaten fish eggs.

The majority of individual animals eaten were tadpoles; the exact number could not be ascertained but was conservatively estimated as 35. Other items, in order of decreasing frequency, were 11 metamorphosed tree toads (*Hyla regilla* and *H. arenicolor*), 4 fish, 1 toad (*Bufo*), 1 worm, and 1 mass of fish eggs.

I discount Stephens' statement (*loc. cit.*) that this garter snake feeds upon insects, as no specific instances are cited and no corroborative data are supplied by other observers. Insect remains found in snake stomachs may be residual from the bodies of small insectivorous vertebrates preyed upon by the snakes.

Klauber's note (1924:16) of an individual "hunting *Hyla* in a marsh at 8:00 P.M." is suggestive of crepuscular or nocturnal foraging in *hammondii*, whereas all observations on other forms indicate that they are strictly diurnal, and do not forage after sunset. The warmer climate within the range of *hammondii* would favor crepuscular habits, and the increased activity of *Hyla* after sunset would also favor such tendencies. The relatively large eyes of *hammondii* are of possible adaptational significance in this connection.

Evidently *hammondii* resembles other members of the Hydrophila group in being closely restricted to the vicinity of stream beds which afford a permanent water supply. Apparently it is somewhat less aquatic than *hydrophila, couchii*, or *gigas*. Although all food recorded was found in the near vicinity of water, the adult *Hyla* were probably not caught in the water by the snakes.

Within the range of *hammondii* as indicated above, most of the watercourses are small and tend to go dry at certain times of year, leaving series of disconnected pools. Under such conditions water temperatures become unfavorably high for some kinds of aquatic life. Fish are mostly absent, especially at lower elevations, and the few kinds present are small. *Dicamptodon* does not occur at all in the range of *hammondii; Triturus* is not common within its range and is mainly confined to the northern part; *Rana boylii* is not found south of the San Jacinto Mountains, and hence does not occur in much of the area occupied by *hammondii*. Most of the forms upon which *hydrophila* and *couchii* depend for food are thus absent where *hammondii* occurs.

Tree toads, on the contrary, are more available to *hammondii* than to other members of the Hydrophila group because they are more closely restricted to a streamside habitat within its range than they are farther north, and because two species occur within its range. *Hyla arenicolor* does not occur within the ranges of other members of the Hydrophila group, but is found throughout most of the range of *hammondii*. It is notoriously restricted to the margins of ponds and streams, usually in rocky canyons. *Hyla regilla* also occurs throughout the range of *hammondii*. Linsdale (1932:353), writing of *Hyla regilla* in Lower California, remarked that it seemed to be closely restricted to the vicinity of water there, apparently differing in habits from populations farther north as a result of the more arid climate. Probably the same is true of populations occurring in southern California, since the climate is prevailingly arid there also. Thus in the range of *hammondii* the tree toad occupies a streamside habitat and replaces other more aquatic forms in the food of these snakes.

Although most of the food items contained by the specimens examined were tadpoles, it must be remembered that this food is available only during certain seasons. Metamorphosed tree toads probably constitute most of the food.

Records of occurrence.—Specimens examined, 261; in the collection of L. M. Klauber (except where otherwise indicated), from the following localities:

California. *Monterey County:* Carmel Valley, 2[3][*]; 4 miles west of Salinas, 1[1]; Soledad, 1[5]; ¾ mile south of San Lucas, Nacimiento River, 2[2]; San Antonio Creek near Mission San Antonio, 1[3]; Tassajara Creek, 3[6]; Church Creek, 1[6]. *San Benito County:* San Benito River near Hernandez, 1[1]; 6 miles east-southeast of San Benito, 1[1]; 1 mile east of summit of San Benito Mountain, 1[1]. *San Luis Obispo County:* Oceano, 1[2]. *Santa Barbara County:* Santa Inez River, 1500 feet, 1[1]. *Ventura County:* Sespe Canyon, 5 (1[5]); Sespe, 6 (5[2]); Fillmore, 6[2]; Santa Paula, 1[3]. *Los Angeles County:* Rock Creek Canyon, 1[2]; Placenta Canyon near Newhall, 1; Crystal Lake, 1; north fork of San Gabriel River, 2000 feet, 2; west fork of San Gabriel River, 3000 feet, 3 (2[1], 1[2]); Monrovia Canyon, 1; Arroyo Seco, 1; Las Flores Canyon, Santa Monica Mountains, 2[1]; Avalon, Santa Catalina Island, 1[2]; Los Angeles, 1[2]. *San Bernardino County:* Santa Ana River, 3 (2[1], 1[3]); Victorville, 4 (2[1], 1[2]); Metcalf Bay, Big Bear Lake, 1; Deep Creek, 2[5]; San Bernardino Mountains, 6[3]; Ontario, 3[3]; Slover Mountain near Colton, 1[1]; San Bernardino, 11[3]. *Riverside County:* Riverside, 2[3]; Cabazon, 1[1]; Tahquitz Valley, 8000 feet, 1[1]; San Jacinto Valley, 8[3]; Idyllwild, 1; Santa Ana Mountains, 1; Murray Canyon, 1; mouth of Palm Canyon, 1[1]; Kenworthy, 4500 feet, 1[1]. *Orange County:* San Juan Hot Springs, 1. *San Diego County:* Palomar, 1; Escondido, 1; San Felipe Wash, 1; Banner, 1; Banner Grade near Julian, 1[4]; Lake Hodges, 1; Santa Fe Ranch, 2; Cuyamaca, 1[4]; Shady Dell, 1[4]; Poway, 1; El Capitan, 4; Cold Spring above Green Valley, 1; Del Mar, 1; San Clemente Canyon, 1[4]; La Mesa, 1; Wildwood Glen, Descanso, 1; Pine Valley, 13 (2[4]); Laguna, 13; Laguna Mountain, 16 (13[4]); Japatul, 1[4]; San Diego, 8 (3[4], 1[5], 1[3]); East San Diego, 1; Chula Vista, 1; Dulzura, 1[1]; Deerhorn Flat, 8 (2[5]); Nestor, 1; 12 miles east of Imperial Beach, 1; Carrizo Springs, 2[4]; Mission Valley, 3; Cuayamaca Mountains, 4 (2[2], 1[4]); Upper Doane Valley, 3; Johnson Creek ½ mile from Boulder Creek, 1; Lees Canyon, 1[4]; Adobe Falls, 1[4]; Moreno, 1[5]; Nobles Mine, 1; Agua Caliente, 1[3]; Oak Grove, 5[3]; near Carlsbad, 1[3]; Santa Isabel Valley, 1[3].

Mexico. *Lower California:* Laguna Hanson in Sierra Juarez, 15; San Jose, 19 (4[1], 3[2]); El Cajon Canyon, 2[1]; La Grulla, 12[2]; San Domingo River above San Antonio, 3; San Antonio Rancho, San Domingo River, 1[1]; San Ramon, mouth of San Domingo River, 2[1]; 8 miles south of Carrizo, 1.

Boulenger (1893:203) records *hammondii* (as "*Tropidonotus vagrans*") from Tia Juana, Lower California, and from San Diego County, California. Hurter (1912:67) records it from Aliso Creek near Laguna Beach, Orange County, California. Klauber (1934:20) recorded it from Carrizo, Imperial County, California.

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[*] Explanation of references: [1] Museum of Vertebrate Zoölogy; [2] California Academy of Sciences; [3] Museum of Natural History, Stanford University; [4] San Diego Society of Natural History; [5] University of Michigan Museum of Zoölogy; [6] Collection of J. von Bloeker, Jr.

Thamnophis digueti (Mocquard)

(Diguet Garter Snake, Lower California Garter Snake)

Thamnophis hammondii, Van Denburgh, 1896:1008 (part)
Tropidonotus Digueti Mocquard, 1899:327 (original description)
Thamnophis ordinoides hammondii, Van Denburgh and Slevin, 1918:256 (part)

Type.—None designated of the six specimens in the Museum d'Histoire Naturelle, Paris, upon which the original description was based, collected at San Ignacio (hereby designated as the type locality) and Mulegé, South District, Lower California, Mexico, by M. Léon Diguet.

Range.—Permanent streams of Sierra de la Giganta, Lower California, Mexico; at present known from only three widely separated localities of that general region: San Ignacio, Mulegé, and Comondú (see fig. 12, p. 74).

Diagnosis.—Maximum number of scale rows on anterior part of body ordinarily 21 (rarely 23), the 5th, when 21 are present, continuous from head back to mid-body; supralabials usually 8, 8, occasionally increased to 9 on one or both sides; infralabials 10, 10 (rarely 11); preocular on each side divided into two plates by horizontal suture; no trace of dorsal stripe; lateral stripe absent or not distinct from ventral coloration; dorsolateral black spots almost entirely confined to skin between scales, small, widely separated, inconspicuous, and hardly discernible except when skin is stretched; supralabials pale below, dusky above, marked posteriorly with faint black wedge marks; top of head uniformly colored; no parietal spots; no black marks in temporal region; gastrosteges average fewer than 161 in males and fewer than 154 in females; chin dull white, with no black markings along sutures separating infralabials; muzzle pointed; contact of either nasal with rostral usually equals or exceeds combined contact of both internasals with rostral.

Coloration.—Description of adult female (alcoholic), Mus. Vert. Zoöl. No. 13790, from San Ignacio:

Top of head uniformly colored, nearest Light Grayish Olive, tending toward Deep Olive-Buff; sides of head dull with no contrasting markings, mainly of same color as top of head but paler in region of mouth; 1st, 2d, 3d, 4th, and 5th supralabials, and lower portions of 6th, 7th, and 8th of approximately the same color; infralabials Olive-Buff or Pale Olive-Buff; skin between supralabials black, but dark markings absent on supralabial scales; body uniformly colored dorsally with no markings visible, between Grayish Olive and Dark Olive-Buff (slightly paler than Pale Russian Blue where outer epidermal layer of scales is rubbed off); lateral stripe not developed; scales of 2d and 3d rows above gastrosteges Olive-Gray; dull color of dorsal surface blends gradually into pale ventral coloration; genials and scales between and behind them Ivory Yellow; ventral surface gradually darkening posteriorly, nearest Gull Gray, gastrosteges clouded with Dark Gull Gray along their anterior margins; pale color of chin extends dorsally in neck region nearly to level of mouth, but gradually blends into darker color of dorsal surface.

Comparisons.—Although *digueti* does not intergrade with any other form, its closest relationship is obviously to *T. hammondii*, from which it differs in the following respects: dorsal black markings much reduced; no trace of conspicuous black crescentic neck markings found in *hammondii;* dorsolateral body spots hardly noticeable except when skin is stretched, though more noticeable in young than in adults; parietal spots absent, as opposed to bright yellow spots in *hammondii* (except in old adults, specimens taken shortly before ecdysis, or those discolored by preservative); no black edges along sutures separating infralabials, whereas such marks are present in *hammondii;* both preoculars nearly always divided, whereas in *hammondii,* although divided in majority of individuals, they are frequently single on one or both sides; gastrosteges and urosteges less numerous (see p. 84); stripes absent; dull ground color blends gradually into paler color of ventral surface, whereas in *hammondii* conspicuous pale lateral stripes are present for full length of body and usually vestige of dorsal stripe is present as dash of yellow on neck; uniformly dull brown dorsal surface and lighter yellowish ventral surface impart appearance strikingly like that of western yellow-bellied racer, at least in preserved specimens; suture separating 6th and 7th supralabials more nearly vertical (average 73°), whereas in *hammondii* it slants obliquely forward (average 64°); number of supralabials occasionally increased to 9 by dividing of 3d on one or both sides; of the 6 original specimens, one had the formula 9, 9, another 9, 8 (Mocquard, 1899:327), whereas in *hammondii* there are almost invariably 8 supralabials on each side.

Remarks on nomenclature and systematics.—In the original description of *digueti* Mocquard stated (1899:321): "C'est avec *Tr. Hammondii,* Kenn. que *Tr. Digueti* paraît avoir le plus d'affinités; il s'en distingue également par ses deux préoculaires et sans doute par d'autres particularités d'organisation; mais comme le Muséum ne possède pas *Tr. Hammondi* je n'ai pu établir de comparaison entre le deux espèces."

As has already been shown, however, the number of preoculars does not constitute a constant difference between *hammondii* and *digueti.* Previous writers who have published accounts of *hammondii* have had no specimens of *digueti* available for comparison, and since the time of its original description it has generally been considered synonymous.

In some of its characters—suppression of stripes and other markings—*digueti* represents a further development of the characters which distinguish *hammondii* from the subspecies of *T. ordinoides.* It is a specialized peripheral form of the *ordinoides* artenkreis within the genus. However, in certain of its characters it is more conservative than *hammondii:* it has a smaller eye and its posterior genials are shorter.

Geographic variation and intergradation.—No geographic variation can be demonstrated with the specimens now available, since all but one are from the same locality. Obviously, intergradation with other forms does not occur, because the known range of *hammondii,* the closest form structurally and geographically, is separated from that of *digueti* by nearly 300 miles of low-lying arid region in the central portion of the peninsula of Lower California, which forms an effective barrier against the distribution of garter snakes.

Habits and habitat.—Of the specimens in the Museum of Vertebrate Zoölogy, C. C. Lamb recorded (MS) that one from San Ignacio was brought to him by a boy who found it near the stream; another was found crawling on the ground under a mesquite tree. One collected at Comondú was caught in a mousetrap at the edge of tules at the creek in the canyon bottom.

Three of the specimens from San Ignacio had eaten 2 metamorphosing *Hyla regilla* and 2 small fish.

Although insufficient to show the range of feeding habits or the kind of food preferred, these data seem to indicate aquatic foraging in *digueti,* which probably resembles other forms of the Hydrophila group, and especially *hammondii,* in this respect.

Records of occurrence.—Specimens examined, 51, from two localities, both in South District, Lower California, Mexico: San Ignacio (Mus. Vert. Zoöl., 16, Univ. Mich. Mus. Zoöl., 23, Klauber, 9. San Diego Soc. Nat. Hist., 2); Comondú (Mus. Vert. Zoöl., 1).

In his original description Mocquard records one from Mulegé and five from San Ignacio. San Ignacio and Comondú are both in the Pacific drainage of the peninsula and are about

80 miles apart; Mulegé lies between these on the gulf of the east side of the peninsula. Thus, *digueti* has an extensive range in southern Lower California. It is to be expected that further collecting will show its range to extend beyond these limits.

THE HYDROPHILA GROUP

The Hydrophila group includes a series of five closely related forms, *hydrophila, couchii, gigas, hammondii,* and *digueti. T. digueti* is narrowly restricted in range and well isolated from the form geographically nearest it, which is its closest relative. It has distinctive characters of coloration and is therefore specifically distinct, though but weakly differentiated. *T. hammondii* is likewise classed as a species because it has trenchant characters, and its range at present is separated from that of *couchii* by an uninhabitable region. However, the morphological resemblance and presumably the genetic relationship between *hammondii* and *couchii* is obviously close; mutual trends toward intergradation are found in certain characters where the ranges of these two forms approach each other. *T. o. couchii, gigas,* and *hydrophila* have geographically continuous ranges and intergrade completely. Members of this group are highly aquatic in their habits; they depend on the water for escape from enemies, and find their food in it.

Characters distinctive of this group, including habits, coloration, and structure, appear to be directly correlated with an aquatic habitat. The bright dorsal stripe, distinctive of most forms of *Thamnophis,* is partly or completely suppressed; bright colors are lacking, and the pattern is a checkered or dull monotone. Unlike many other members of the genus these snakes do not ordinarily forage in dense vegetation, and a bright yellow stripe would have no protective value but would only render them conspicuous in the open habitat which they occupy; they spend much of their time on bare rocks at the edges of streams. In such situations the dull coloration is concealing. The shape of the head is conspicuously modified; the muzzle is elongate and pointed; the head is narrow across the temporal region and but little wider than the diameter of the neck. This is probably an aquatic adaptation making the animal streamlined and facilitating rapid passage through the water. As compared with members of other groups these snakes have the posterior supralabials, especially the 6th, much reduced in size. These scales cover the large salivary glands of the upper jaw, and probably their reduced size in snakes of the Hydrophila group is a direct consequence of reduction in the size of these glands. Nearly all the food is captured in the water and often is swallowed under water. The smooth-skinned, slimy animals with streamlined bodies which these snakes prey upon are easily swallowed without the lubrication provided by a copious salivary secretion. In aquatic animals salivary glands are usually reduced in size; in the Hydrophila group this reduction has occurred, and it is reflected in the size and shape of the supralabial scales.

These snakes hunt mainly by sight, since the prey is found under water where the olfactory sense, an important aid to foraging in some *Thamnophis,* probably cannot function. However, it is possible that olfactory stimuli may be received through Jacobson's organ in subaquatic foraging, for it has been noted that snakes hunting under water do not keep their mouths tightly closed.

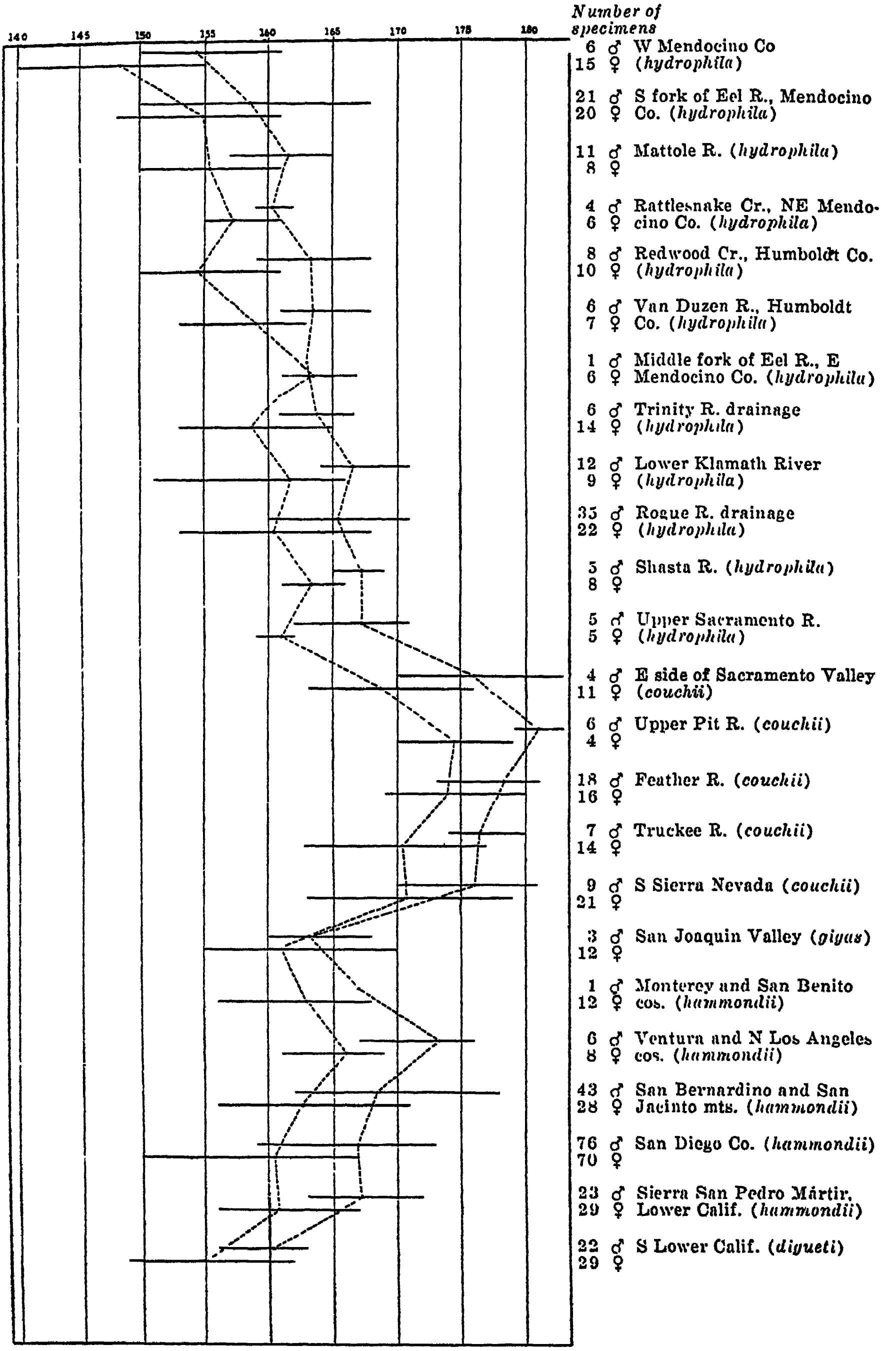

Fig. 13. Numbers of gastrosteges in populations of the Hydrophila group. Note that gastrosteges are most numerous in *couchii*, and that *gigas* is sharply set off from *couchii* in having fewer gastrosteges; that in *hydrophila* numbers of gastrosteges are much reduced, especially in populations confined to the coastal fog belt, but are increased in populations adjacent to the ranges of *biscutatus* (Shasta River) and *couchii* (upper Sacramento River), which show intergradation; also that *digueti* has fewer gastrosteges than *hammondii*.

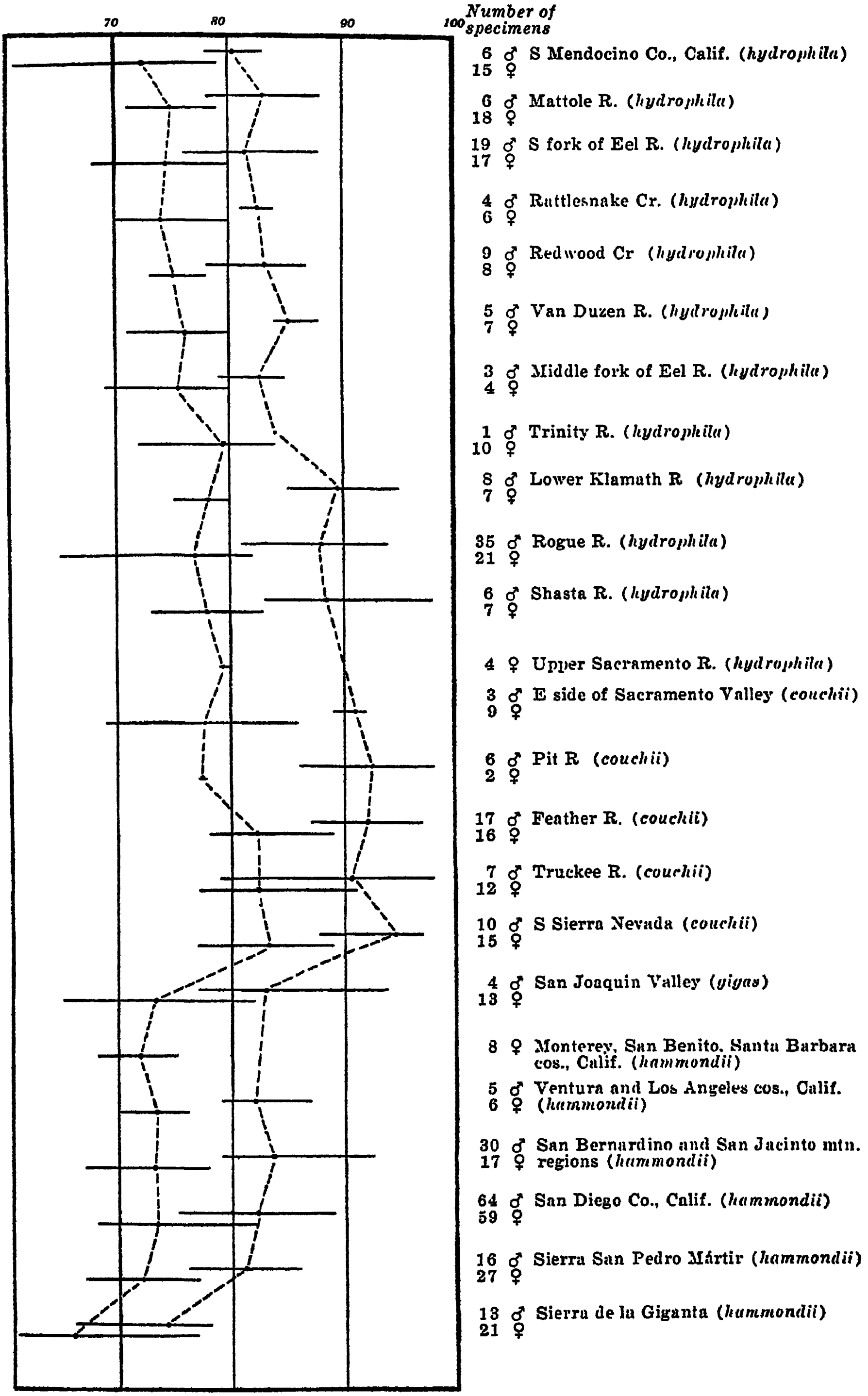

Fig. 14. Numbers of urosteges in the Hydrophila group. Note that geographic trends follow closely the number of gastrosteges (see fig. 13).

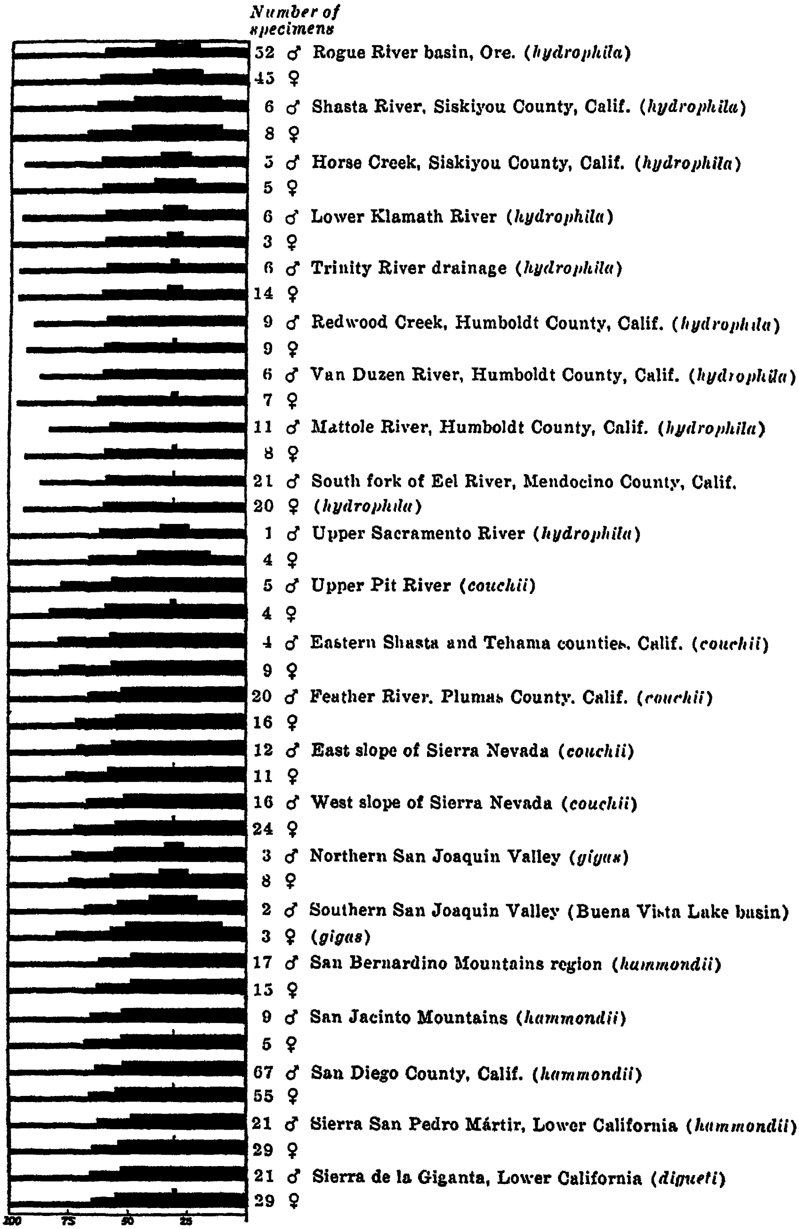

Fig. 15. Diagram showing average lengths and positions of scale rows which vary in the Hydrophila group (plotted for left side of body only). In each polygon longest (basal) column represents "7th" scale row, the one above it represents "4th" row; third column from bottom represents "6th" row, and top or fourth column represents "5th" row of the original 23. Right-hand margin of figure represents head ends of snakes, and left-hand margin represents posterior ends of bodies. Note that rows are suppressed in the same sequence as in the Elegans and Ordinoides groups, that they center at approximately the same point; that females have, on the average, longer rows than have males; and that greatest reduction has taken place in populations of *hydrophila* endemic to streams of the coastal fog belt; also, that *couchii*, *hammondii*, and *digueti* sometimes have vestiges of the "5th" scale row, but that this row is well developed only in *gigas*.

The eyes are relatively large in snakes of this group but vary in the different races. In *hammondii* the extreme of large eye size is attained. In *digueti* and *couchii* the eyes are nearly as large; they are smaller in *hydrophila* and *gigas.* In all of them the pupil is relatively small and the iris is uniformly colored, sometimes hazel but more often some shade of pale brown, gray, or yellow.

TABLE 4

NUMBERS OF PREOCULARS IN POPULATIONS OF THE HYDROPHILA GROUP

Four preoculars (2 on each side) is the normal number in *digueti* and the most frequent number in *hammondii*; *couchii*, especially on the east side of the Sierra Nevada, occasionally has 4 preoculars; *hydrophila* normally has but 2 preoculars except in that part of its range where it is intergrading with *biscutatus* (Shasta River); *gigas* likewise normally has but 2.

Population	Number of specimens	Number of preoculars		
		2	3	4
Coos and Douglas cos., Ore. (*hydrophila*)	16	.88	.06	.06
Rogue River basin, Ore. (*hydrophila*)	103	.85	.07	.08
Smith River basin (*hydrophila*)	5	.80	—	.20
Shasta River basin (*hydrophila*)	13	.38	.16	.46
Lower Klamath River (*hydrophila*)	24	.87	.13	—
Humboldt, Mendocino, Trinity and western Shasta cos., Calif. (*hydrophila*)	131	.97	.02	.01
Pit River (*couchii*)	9	.33	.33	.33
Shasta and Tehama cos., Calif. (*couchii*)	19	.84	.11	.05
Feather River (*couchii*)	36	.72	.19	.09
W slope Sierra Nevada (*couchii*)	49	.89	.02	.09
E slope Sierra Nevada (*couchii*)	34	.38	.12	.50
San Joaquin Valley (*gigas*)	13	.92	.08	—
Monterey and San Benito cos., Calif. (*hammondii*)	14	—	.22	.78
Los Angeles Co. and San Bernardino Mts. (*hammondii*)	31	.16	.10	.74
San Jacinto Mts. (*hammondii*)	12	.58	.17	.25
San Diego Co. (*hammondii*)	127	.19	.26	.55
Sierra San Pedro Mártir (*hammondii*)	48	.14	.21	.65
Sierra de la Giganta (*digueti*)	50	.02	.10	.88

Large eye size in *hammondii* may be correlated with crepuscular foraging, and also with its open habitat, since it occurs in a relatively arid region where streamside vegetation is scanty. In some other respects it is also the most divergent and specialized of the entire group, and it may be regarded as showing the extreme development of large size of eye which is common to the entire series. In *gigas*, which probably occurs in a more open habitat than any of the other forms, the smaller eye size is partly a matter of relative growth, since the eye is relatively smaller in large individuals. The more conservative eye size of *hydrophila* is regarded as primitive and showing relationship to members of the Elegans and Ordinoides groups.

All five members of the Hydrophila group are much alike in mannerisms

TABLE 5

NUMBERS OF SUPRALABIALS IN THE HYDROPHILA GROUP

Note that 16 (8 pairs) is the usual number in all the forms; that in *couchii* and *gigas* and especially in *digueti* there are slight tendencies to increase this number, and that in *hydrophila* from the coastal region there is a slight tendency toward reduction in numbers.

Population	Number of specimens	Number of supralabials			
		15	16	17	18
Rogue R. basin, Ore. (*hydrophila*)	71	—	1.00	—	—
Siskiyou Co., Calif. (*hydrophila*).	31	.03	.97	—	—
Humboldt Co., Calif. (*hydrophila*)	69	.04	.91	.01	—
Mendocino Co., Calif. (*hydrophila*)..................	83	.01	.98	.01	—
Shasta and Tehama cos., Calif. (*couchii*)....................	24	—	.79	.17	.04
Plumas Co., Calif. (*couchii*).....	36	—	.83	.11	.06
Sierra Nevada (S of Plumas Co.) (*couchii*)....................	80	—	.88	.12	—
San Joaquin Valley (*gigas*)......	18	—	.94	—	.06
S Calif. and N Lower Calif. (*hammondii*).................	245	—	1.00	—	—
S Lower Calif. (*digueti*).........	50	—	.76	.22	.01

TABLE 6

NUMBERS OF INFRALABIALS IN POPULATIONS OF THE HYDROPHILA GROUP

Note that 20 (10 pairs) is the usual number in *hydrophila*, *gigas*, *hammondii*, and *digueti*; that in typical *couchii* the number is usually increased to 22 (11 pairs); that in *gigas* there is also a tendency toward increase in numbers; that in *hydrophila* there is a slight tendency toward reduction to fewer than 20, especially in the coastal region; that *hammondii* is extremely stable in this character.

Population	Number of specimens	Number of infralabials						
		18	19	20	21	22	23	24
Rogue R. basin, Ore. (*hydrophila*)	71	.04	.04	.87	.01	.04	—	—
Siskiyou Co., Calif. (*hydrophila*).	28	—	.11	.89	—	—	—	—
Humboldt Co., Calif. (*hydrophila*)	69	.03	.12	.78	.06	.01	—	—
Mendocino Co., Calif. (*hydrophila*)	83	.07	.12	.77	.01	.01	.01	—
Shasta and Tehama cos., Calif. (*couchii*).....................	24	.04	—	—	.08	.79	.08	—
Plumas Co., Calif. (*couchii*)......	36	—	—	.42	.19	.36	.03	—
Sierra Nevada (S of Plumas Co.) (*couchii*).....................	79	.01	.06	.65	.09	.19	—	—
San Joaquin Valley (*gigas*).......	17	—	.12	.47	.29	.12	—	—
S Calif. and N Lower Calif. (*hammondii*)..................	245	.01	.03	.96	—	—	—	—
S Lower Calif. (*digueti*)..........	50	.08	.02	.86	.04	—	—	—

and behavior, being active in escaping and aggressive when caught or cornered. Under such circumstances one will assume a threatening attitude by flattening its head and body, and will strike and bite savagely when an opportunity is presented. Such instinctive tendencies may have developed concurrently with the adoption of an exposed habitat, which is typically the bare rocks at the edge of the water. In this habitat these snakes are readily found by predators, especially by wading birds. Vigorous self-defense on the part of a snake might intimidate such an enemy, at least momentarily, affording the snake an opportunity to escape.

Available data indicate that *hammondii* is less aquatic in foraging than are the other forms, probably because aquatic animals are less abundant in the region it occupies, where streams have fluctuating and uncertain water supply, and water temperatures are often unfavorably high.

The five forms differ in scale characters, and definite trends are apparent. Maximum numbers of gastrosteges, urosteges, and infralabials occur in the race *couchii*, which is central in its distribution with respect to the other forms. The race *gigas*, which is also central in distribution, has the maximum number of scale rows for this group and for the genus. The peripherally distributed forms of the group, *hammondii*, and especially *hydrophila* and *digueti*, are characterized by reduction in numbers of ventrals; in *hydrophila* the number of scale rows, as well as the gastrosteges and urosteges, is reduced. The subspecies *couchii* and *gigas* also attain larger size than the other races. In the Hydrophila group, as in the Ordinoides and Elegans groups within the species, there are, apparently, tendencies toward dwarfing, and toward reduction in numbers of scales in the northern and southern parts of the range.

Thamnophis ordinoides atratus (Kennicott)

(Coast Garter Snake, Single-striped Garter Snake)

Eutainia ordinoides, Baird and Girard, 1853:33
Eutainia atrata Kennicott, 1860*a*:296 (original description)
Eutaenia elegans ordinoides, Cope, 1892:654
Eutaenia infernalis infernalis, Cope, 1892:657
Eutaenia infernalis vidua Cope, 1892:658
Tropidonotus ordinatus var. *infernalis*, Boulenger, 1893:207
Thamnophis elegans, Van Denburgh, 1897:207 (part)
Eutaenia elegans elegans, Brown, 1903:288 (part)
Eutaenia elegans infernalis, Ditmars, 1907:226, pl. LXIX, fig. 2
Thamnophis ordinoides ordinoides, Ruthven, 1908:147 (part)
Thamnophis ordinoides, Thompson, 1915:351
Thamnophis ordinoides atratus, Van Denburgh and Slevin, 1918:224, pl. 9 (part)

Type.—Adult male, U. S. Nat. Mus. No. 970-A, collected at San Francisco, California, by R. D. Cutts. (Hereby selected from the two cotypes upon which the original description was based.)

Range.—Coast counties of California from Orick, Humboldt County, south to Santa Inez River, Santa Barbara County; mainly confined to seaward side of immediate coast ranges, within the fog belt. Eastward records are: Clear Creek, Siskiyou County; Cobbs, Humbodlt County; near Cummings, Mendocino County; Mount Diablo, Contra Costa County; Gilroy Hot Springs, Santa Clara County; and Pinnacles, San Benito County (see fig. 16).

Diagnosis.—Maximum number of scale rows on body 21 or 19, of which 5th (when 21 are present) is short, not continuous from head back to mid-body; 4th extends from head at least two-thirds of distance to anus; supralabials 8, 8; infralabials 10, 10; preoculars, 1, 1; muzzle blunt; internasals broadly in contact with rostral, their combined contact usually exceeding contact of either nasal with rostral; genials subequal; dorsal stripe distinct, bright yellow; sometimes widened to cover 3 scale rows for most of its length; dorsal ground color dark gray or brown, showing superimposed black spots faintly; lateral stripe dull yellow, *or red*, or entirely absent; red markings often present on ventral surface or dorsolateral area; supralabials yellowish, often dull colored, usually without well-developed wedge marks; chin often yellow; ventral surface blotched medially with yellow, or pink; iris pale, almost uniformly colored in southern part of range (or dark with pale yellow rim round pupil in northern part of range).

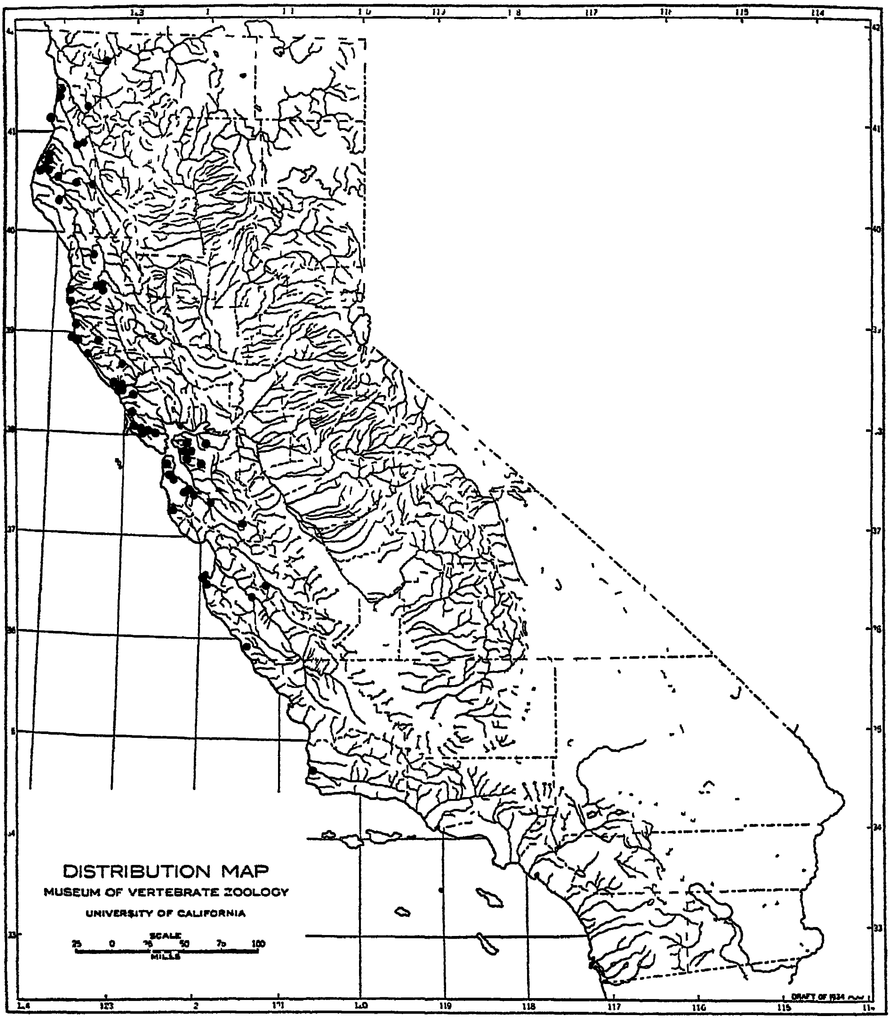

Fig. 16. Range of *Thamnophis ordinoides atratus* (dots show localities from which specimens have been examined) in coastal region of California.

Coloration.—Description of freshly killed adult female, Mus. Vert. Zoöl. No. 19119, from Lake Merced, San Francisco County, California.

Top of head Yellowish Olive with faint reticulations of black along parietal suture; supralabials Chamois with faint grayish suffusion; 4th, 5th, 6th, and 7th with narrow black margins posteriorly which lack the form of wedge marks and do not continue downward to edge of mouth; iris yellowish, heavily dotted with fine pigment granules which cause it to appear gray or olive; dorsal stripe Light Cadmium, distinct for full length, three scales in width at anterior end of body and for about one-sixth of distance to posterior end of body, encroaching upon posterior edges of parietal plates, and immediately behind them nearly 5 scale rows wide; scales of dorsolateral area Buffy Olive along central portions, black along edges; lateral flecks Pale Olivine; skin of dorsolateral area otherwise black; lateral stripes Chamois, lightly dotted with black, scales near anterior ends edged with yellow; last 2 infralabials Chamois, rest of chin and first 11 gastrosteges Cream Buff; other gastrosteges and urosteges Cream Buff intermixed with areas of Pale Green-Blue Gray or Clear Green-Blue Gray in an irregular mosaic; in several spots darker color is nearly black, at other places the Cream Buff is brightened to Light Orange-Yellow.

Individual variation in coloration appears to be greater on the San Francisco peninsula than at any other one place in the range of the species. Other specimens collected at the same time and place as the one described above were found to be colored as described below: Dorsal stripe Apricot Yellow in one, Citron Yellow in one, Capucine Yellow (tending toward Ochraceous-Orange) in one, Ochraceous-Orange in one; dorsal ground color nearly black in one with Scarlet blotches covering its lower half, Buffy Olive and black in one, Sepia and black in one; chin Massicott Yellow in one, nearly white in two; gastrosteges Oural Green with several Scarlet spots in one, Chartreuse Yellow (shading into Asphodel Green on tail) in one, Gnaphalium Green with Corydalis Green in central portions of gastrosteges in one, Olivine in one.

Comparisons.—*T. o. atratus* intergrades with *ordinoides* and *elegans* and its range overlaps those of *hydrophila* and *hammondii* without intergradation. It has already been compared with *elegans*, *hydrophila*, and *hammondii* in the accounts of those forms.

Compared with *ordinoides*, *atratus* differs in having 8 rather than 7 pairs of supralabials, 21 rather than 19 scale rows, more gastrosteges and urosteges on the average (see p. 105); dorsal stripe bright yellow, not red, dull yellow, or entirely lacking as it often is in *ordinoides;* iris often pale rather than heavily pigmented as in *ordinoides;* bright red coloring on ventral surface, lateral stripes on dorsolateral region in combination with bright yellow dorsal stripe, a pattern scheme not found in *ordinoides;* chin sometimes bright yellow rather than whitish as in *ordinoides;* supralabials sometimes yellowish rather than pale olive as in *ordinoides;* gastrosteges sometimes marked medially with yellow blotches that are absent in *ordinoides;* head broader, more distinct from neck; average size larger (see p. 8).

Remarks on nomenclature and systematics.—The original description of *atratus* was apparently based on two specimens in the National Museum from San Francisco collected by R. D. Cutts, both catalogued under the number 970. Of these the larger, No. 970-A, is a male, which has 153 gastrosteges, 78 urosteges, and a scale formula of 19-19-17-15, a total length of 24¾ inches, and a tail length of 6⅞ inches; No. 970-B, apparently a male, has 149 gastrosteges, 81 urosteges, scale formula of 19-19-17-15, a total length of 17 inches, and a tail length of 4¼ inches, as I am informed by Dr. Stejneger.

According to Brown (1903:295), these same specimens served as a basis for Cope's description of *Eutaenia infernalis vidua* (Cope, 1892:658).

In an early paper, Van Denburgh (1897:207) did not recognize this form as distinct from *elegans* and included both under the latter name.

Ruthven (1908:147) included *atratus* in the subspecies *ordinoides*, although he indicated the principal differences between *atratus* and typical *ordinoides* as it occurs north of Humboldt County.

Van Denburgh and Slevin (1918:224) defined *atratus* approximately as understood by me. However, many of the specimens listed by them are of other forms. Most of these wrongly identified specimens are *T. o. hydrophila* from Humboldt and Mendocino counties, but Calif. Acad. Sci. Nos. 29224 and 29227 from Crescent City (1918:234) are *Thamnophis sirtalis*. Stanford Mus. Nat. Hist. Nos. 4313 and 4434 from Anderson, Shasta County, are *T. o. elegans*.

Concerning intergradation between *ordinoides* and *atratus*, Van Denburgh and Slevin wrote (1918:223): "So far as specimens examined by us show, this intergradation occurs only in Del Norte County, California, where the ranges of the two forms meet and perhaps overlap slightly. Many of the specimens from this county are typical of either one or the other subspecies,—*ordinoides* or *atratus*,—and most of the intergrades seem to be nearer to the latter type than to the former." They further commented (1918:234): "Certain specimens from Requa and Crescent City in Del Norte County, California, show intergradation between *T. o. atratus* and *T. o. ordinoides*. This is apparent in the reduction in the number of the upper and lower labials, and, sometimes, of the gastrosteges. Some of the specimens from these localities are fairly typical *T. o. atratus*, and nearly all are closer to that form than to *T. o. ordinoides*."

Geographic variation and intergradation.—With additional specimens from these same localities in Del Norte County, and from new localities in the same general region, I find the same type of intergradation as that described by Van Denburgh and Slevin (*loc. cit.*). Specimens colored like *atratus* of the San Francisco Bay region may be found in the same localities with red-striped individuals typical of the southern population of *ordinoides* in appearance. No red-striped specimens have been found south of the Klamath River, though there are several such specimens in the Museum of Vertebrate Zoölogy and the California Academy of Sciences from near Requa on the north side of the river. The northernmost specimen having an *atratus* pattern was collected on the California coast at the Oregon state line.

Although the characteristic color patterns of the two forms do not show gradual transition from one to the other, such merging is shown in part by other characters: labials, gastrosteges, urosteges, eye color, and shape of head. In the region of intergradation the population is highly heterogeneous in several characters, thus differing from intergrading populations between other races, which are usually remarkably uniform in characters in any given locality. Because of this uneven intergradation and the distinctness of the two forms, it seems probable that at some time in the past the ranges of *atratus* and *ordinoides* were separated. Some individuals are intermediate and combine the characters of the two forms, but in general the specimens having a yellow stripe also tend to have a higher number of gastrosteges, and possess other characters peculiar to *atratus*, while those having a red stripe generally tend to resemble *ordinoides* most closely in other characters as well. Possibly these forms represent closely related but distinct species which hybridize in the region where their ranges overlap. For positive determination of their genetic relationship, a large number of gravid females from the region of intergradation should be collected and variation in their broods of young studied.

Because these two forms are obviously closely related, because their habits and habitats are similar, because their ranges meet, and because intermediate specimens occur, they are here considered subspecies of the same species.

Specimens from northern Humboldt County show a heavy preponderance of *atratus* characters, although in several respects they depart from the characters of typical *atratus* in the direction of *ordinoides*. This is especially true of series taken farthest north, at Prairie Creek and Redwood Creek. They resemble *ordinoides* in having narrow heads not distinct from the neck, anterior supralabials small and crowded or occasionally reduced by fusion to 7 pairs as in *ordinoides;* infralabials usually fewer than 10 pairs; dark longitudinal mark developed in temporal region; supralabial wedge-marks not well developed; irises dark brown. These specimens have a dark ground color, bright yellow dorsal stripe, and red spots on the dorsolateral area.

Specimens from southern Humboldt County resemble those described above. The dorsal stripe is yellow and distinct in all of them but it is not as bright as in specimens from the southern part of the range; rather, it is dull and waxy in appearance. The lateral stripe is pale, yellowish, or gray, and distinct in all. Many have rusty reddish markings on the dorsolateral area which are highly variable in extent. Irregular red markings are likewise present on the ventral surface in some, but are usually small and inconspicuous. As compared with other series from most parts of the range, Humboldt County specimens have more gastrosteges and urosteges, and therefore do not show intergradation between typical *atratus* and *ordinoides*. Evidently these snakes tend toward *T. o. elegans*, which extends from the inner coast ranges westward along South Fork Mountain nearly to the coast. Three specimens from the Van Duzen River at Cobbs near the eastern border of Humboldt County show intergradation and are intermediate between *atratus* and *elegans* in nearly all respects in which the two forms differ; they seem nearer *elegans* in having wide heads with short, blunt muzzles, well-developed supralabial wedge marks, black dorsal ground colors with bright yellow dorsal stripes, distinct yellow lateral stripes, and pale ventral surfaces suffused with pinkish coloring. These specimens are placed with *atratus* mainly because they have minute red markings at irregular intervals along the lateral stripe and the edges of the dorsal stripe. Such markings are not found in *elegans*. Specimens taken a few miles farther east, at various points along the Mad River, are similar in all respects except that none has (in preservative) any trace of red markings; they have therefore been referred to *elegans*.

A specimen from Rattlesnake Creek, northeastern Mendocino County, is typical in appearance of many individuals occurring much farther south in the San Francisco Bay region: it has a dark, nearly black, ground color, a bright yellow dorsal stripe, and red lateral stripes. Specimens from the immediate coastal region of Mendocino County are characterized by having a low number of gastrosteges—fewer, on the average, than in specimens from anywhere else in the range except the extreme southern portion; and their numbers of urosteges are likewise reduced. These specimens are peculiar in coloration; the ground color is brown, paler than in specimens from other parts of the range, and usually the ventral surface and dorsolateral area are conspicuously marked with red. Of two living adult females collected near Elk, one had dark heavily pigmented irises, with narrow pale inner rims around the pupils, the other had paler, more uniformly colored irises. Evidently the transition from the dark brown, heavily pigmented iris of *ordinoides* and northern populations of *atratus* to the paler, almost uniformly colored iris of southern populations of *atratus* takes place in this general region.

Specimens from Sonoma and Marin counties have relatively high numbers of gastrosteges and urosteges as compared with those from other parts of the range. They likewise have the "6th" scale row present more frequently, and on the average it is longer, especially in Marin County specimens. The ground color is dark brown or grayish brown, frequently marked with red. The ventral surface may be marked with red also. The supralabials are pale gray, or olive, with wedge marks poorly developed or entirely absent.

Specimens from the San Francisco peninsula are extremely variable in coloration. Van Denburgh (1922:820–821) wrote in discussing color variation in *atratus:*

"Certain types of coloration may be pointed out as occurring in groups of specimens. The best known of these color types, perhaps, is that in which the general coloration is dark olive, lateral lines absent, dorsal line yellow and very broad, throat bright yellow, and belly deep olive or slate with or without a median yellow streak. . . . It is not a common style of coloration in this subspecies since we find it more or less well marked in only twenty-nine of three hundred and sixty-three specimens, or 8%. All of these specimens are from the San Francisco peninsula, that is to say from San Mateo, Santa Clara, Santa Cruz and Monterey counties. They, however, share this area with snakes of various other styles of coloration, and all sorts of intermediate specimens are to be found, so that this seems to be merely a peculiar color phase, although restricted geographically to a small portion of the range of this subspecies.

"Specimens from San Francisco and Marin counties usually may be recognized as such by their coloration, which is of a style not peculiar to these areas, but certainly most common there. There are three lines, the dorsolateral region is largely red with dark spots, and the belly is often more or less suffused with bright brick red."

Specimens from the San Francisco peninsula are also peculiar in having few gastrosteges and urosteges; they are particularly distinct in this respect from those taken east of the bay in Alameda and Contra Costa counties. Because of the distinctive characters, both in coloration and scalation, of specimens from populations only a few miles away on opposite sides of the bay, it seems probable that in the past these populations have been completely isolated from the mainland, perhaps on several separate islands, where they have undergone differentiation.

Specimens from the region east of San Francisco Bay, in Alameda and

Contra Costa counties, exceed all other series in numbers of gastrosteges, and also have more urosteges than specimens from other parts of the range. They differ from those of the San Francisco peninsula in having distinct lateral stripes, in lacking heavy black markings on the ventral surface and conspicuous yellow mid-ventral streaks often found in snakes from the San Francisco peninsula, and in having the dorsolateral area less frequently or less extensively marked with red. The ground color is dark in adults, but paler in young, which usually show superimposed black spots distinctly. The lateral stripe is often entirely red. These specimens also have the "6th" scale row present more often, and longer on the average, than in specimens from the San Francisco peninsula or those from the region north of San Francisco Bay. Specimens from the San Francisco Bay region have irises paler than in those from the northern part of the range, and almost uniformly colored, gray, or sometimes greenish.

Specimens from Monterey, San Benito, San Luis Obispo, and Santa Barbara counties are peculiar in having lower numbers of gastrosteges than have the snakes from any other part of the range, except the Mendocino County coast, and they are set off even more definitely by their low numbers of urosteges. In these specimens the "6th" scale row averages longer than in any other series of *atratus*. These specimens have a dark, nearly black ground color, distinct yellowish lateral stripes, pale supralabials, usually with well-developed wedge marks, and broad heads with short blunt muzzles. Red markings are absent except in a few of those from northern Monterey County. The most southern populations of *atratus* thus approach *elegans* closely in characters and general appearance. It seems certain that *elegans* and *atratus* do not now intergrade in southern California. Although their ranges approach each other there, *atratus* is restricted to the fog belt along the coast and *elegans* is restricted to high elevations in the mountains, with an unfavorably arid and warm area intervening. That intergradation occurred in this region in the course of a former moister and cooler climatic cycle when both forms were more widely distributed, seems evident from the close similarity of the two where their ranges approach each other.

Habits and habitat.—Grinnell and Camp (1917:180), Van Denburgh (1922:823), Thompson (1915:359), Grinnell and Linsdale (1936:38), and Ditmars (1907:226) have published data on the habits of *atratus*.

Habitat data are available for 84 individuals. Although these data are difficult to classify, it may be said that 30 snakes (about 36 per cent) were found away from the near vicinity of water, though usually in damp places where thick vegetation provided abundant shelter; 52 (about 62 per cent) were within a few yards of a permanent water supply, and most of these were in dense riparian growths. Only two snakes were seen in the water, and these were not foraging. Individuals were often alarmed in situations where they might easily have escaped into the water, but almost without exception they took refuge beneath plant cover or in holes in the ground. A few individuals were found in dry situations such as chaparral-covered hillsides, but none was found more than a few feet from thick vegetation. In ecologic preferences *atratus* is essentially restricted to meadows with high grass, to riparian thickets, and to clearings with second growth.

Records of feeding available for 59 snakes, mostly preserved specimens, from localities representative of the range of this subspecies include 186 separate items. Slugs had been eaten by 38 (66 per cent); mice (*Microtus*) had been eaten by 6 (10 per cent); lizards (5 *Gerrhonotus* and 1 *Sceloporus*) had been eaten by 6 (10 per cent); salamanders (*Batrachoseps, Ensatina, Aneides*) had been eaten by 3 (5 per cent); fish had been eaten by 3 (5 per cent); snakes (juvenal *Coluber constrictor mormon* and *Thamnophis ordinoides atratus*) had been eaten by 2 (4 per cent); birds (*Zonotrichia leucophrys* and *Spinus* sp.) had been eaten by 2 (4 per cent); fish eggs had been eaten by 2 (4 per cent); a brush rabbit had been eaten by one (2 per cent); and an earthworm had been eaten by one (2 per cent). Of the individual animals eaten 154 (83 per cent) were slugs, 11 (6 per cent) were mice, 6 (3 per cent) were lizards, 3 (2 per cent) were salamanders, 3 (2 per cent) were fish, 3 (2 per cent) were birds, 2 (1 per cent) were snakes, 1 (0.5 per cent) was a brush rabbit, and 1 (0.5 per cent) was an earthworm; masses of fish eggs were found in 2 snakes.

Five of the items consumed, less than 3 per cent of the total, were evidently found under water by the foraging snakes. All others were of strictly terrestrial species. The terrestrial vertebrates frequently preyed upon are mostly of relatively inactive kinds which are easily captured— young mice, nestling birds, alligator lizards, and plethodont salamanders. Cannibalism is probably rare. Adults of *atratus* which fed regularly on lizards in captivity did not molest small young of their own or other subspecies kept in the same cage. The finding of rabbit remains in one stomach was especially remarkable, since the snake containing them was not of adult size.

Records of occurrence.—Specimens examined, 304, in Museum of Vertebrate Zoölogy (unless otherwise indicated), from the following localities, all in California:

Siskiyou County: Klamath River at mouth of Clear Creek, 1 (intergrade with *T. o. ordinoides*). *Humboldt County:* Klamath River at mouth of Bluff Creek, 2; Prairie Creek State Park, 1; Prairie Creek 2 miles north of Orick, 6; east fork of Willow Creek, 4; Redwood Creek at Grays Resort, 1; Trinidad, 2[1][*]; Eureka, 2; Elk River 5 miles south of Eureka, 6; Fernbridge, 1; Ferndale, 1; Rohnerville, 1; Carlotta, 56 (55[1]); 3 miles west of Bridgeville, 1; Cuddabeck, 1; Bull Creek Post Office, 1. *Mendocino County:* Rattlesnake Creek 9 miles southeast of Cummings, 1; Sherwood, 3; Bald Hill, 2; Irishes, 1[2]; Fort Bragg, 6; 6 miles north of Willits, 1; 10 miles north of Willits, 1; Eagles Nest, Noyo River, 1; 3 miles north of Ornbaum Springs, 1; Garcia River ½-mile to 10 miles above mouth, 1[2]; Elk Creek 3 miles south of Elk, 2; Point Arena, 2; Mendocino City, 3 (1[2]); Gualala, 7. *Sonoma County:* Skaggs Springs, 5 (4[1]); Duncan Mills, 4[1]; 7 miles west of Cazadero, 3; Freestone, 3; 1 mile west of Guerneville, 2; Jenner, 1; Austin Creek, 1[1]; Kidd Creek, 1[1]. *Marin County:* 3 miles west of Inverness, 3; Inverness, 1; 1 mile west of Point Reyes Station, 4 (1[1]); Camp Taylor, Papermill Creek, 1; Lagunitas Creek, 1; Inverness Creek, 1; Tocaloma, 5[1]; San Geronimo, 1. *Contra Costa County:* Wildcat Canyon, 4; Walnut Creek, 1; 2 miles south of Lake Orinda, 1; Moraga Valley, 1. *Alameda County:* vicinity of Berkeley, 37; San Leandro, 1; Thornhill Pond, 2; Oakland, 1; Miller Creek, 1. *San Francisco County:* 74 (51[1], 4[3]): Goat Island, San Francisco Bay, 3. *San Mateo County:* Skyline Boulevard near Millbrae Highlands, 1; San Andreas Lake, 1; Menlo Park, 2; Pescadero Creek, 1. *Santa Clara County:* Stanford University campus, 1[1]; San Jose, 3[1]; Gilroy Hot Springs, 3[1]. *Santa Cruz County:* 4[3]. *Monterey County:* Soledad, 1[3]; mouth of Carmel River, 1[4]; 1 mile south of Chalk Peak, 1; North Gate, Seventeen-mile Drive, 1. *San Benito County:* Pinnacles, 1[1]. *Santa Barbara County:* Santa Inez River, 1.

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[*] Explanation of references: [1] California Academy of Sciences; [2] Natural History Museum, Stanford University; [3] University of Michigan Museum of Zoölogy; [4] Collection of J. von Bloeker, Jr.

Thamnophis ordinoides ordinoides (Baird and Girard)

(Puget Sound Garter Snake, Narrow-headed Garter Snake, Red-striped Garter Snake, Small-headed Striped Snake)

Tropidonotus ordinoides Baird and Girard, 1852:176 (original description)
Eutainia leptocephala Baird and Girard, 1853:29
Eutaenia leptocephala, Girard, 1858:151 (part)
Eutainia cooperi Kennicott, 1860*a*:296
Eutaenia atrata, Townsend, 1888:240
Tropidonotus leptocephala, Boulenger, 1893:201
Thamnophis leptocephala, Van Denburgh, 1897:206
Thamnophis leptocephala olympia Meek, 1899:235
Thamnophis rubristriata Meek, 1899:235
Eutaenia sirtalis leptocephala, Brown, 1903:295 (part)
Eutaenia elegans, Ditmars, 1907:224 (part)
Thamnophis ordinoides ordinoides, Ruthven, 1908:147 (part)

Type.—None designated in the original description, which was based on a specimen or specimens "From Puget Sound." I have been informed by Dr. L. Stejneger that no typical material is now in the National Museum.

Range.—Southern Vancouver Island and mainland of southern British Columbia near the coast; southward across Washington and Oregon west of the Cascade Mountains, and into western Del Norte County, California. Closely restricted to the immediate seacoast south of the Oregon state line (see fig. 17).

Diagnosis.—Maximum number of scale rows on body 19, often reduced to 17; or, when 19 are present, the 4th reduced in length, that is, not continuous posteriorly from head back to mid-body; supralabials usually 7, 7; sometimes fewer, rarely 8 on one or both sides; infralabials usually 8 or 9 on both sides, rarely 10; preoculars usually divided in northern part of range (northern Washington and British Columbia), single in southern part (southwestern Oregon and northwestern California); gastrosteges fewer than 155; urosteges fewer than 85; dorsal stripe various shades of yellow, red, or orange, usually well developed, sometimes faint or absent; dorsal ground color black, brown, greenish, or bluish; ventral surface often spotted with bright red, sometimes heavily marked with black (in northern part of range); iris heavily pigmented; pupil with narrow, pale, yellowish border; a dark temporal bar often present; supralabial wedge marks not developed; head narrow posteriorly, not distinct from neck; muzzle blunt; combined contact of internasals with rostral exceeds contact of either nasal with rostral; eye relatively small.

Coloration.—Description of freshly killed adult female (Mus. Vert. Zoöl. No. 18128) from Klamath Glen, Del Norte County, California (typical of the usually red-striped southwestern population).

Ground color Deep Olive-Gray with slight brownish cast, tending toward Drab on top of head and on anterior part of body, shading into Olive-Gray on posterior part of body and tail; parietals closely dotted with black; other cephalic plates more lightly dotted; rostral and nasals and internasals marked with small Vinaceous Rufous blotches; iris dark brown (Chestnut-Brown ?) heavily and unevenly pigmented, with paler yellowish margin around pupil; dorsal stripe Vinaceous Rufous, of irregular width varying from width of one scale to nearly three scales, discontinuous on posterior part of body, where represented by irregularly placed spots; these nearly absent on tail, there represented by seven widely separated spots; lateral flecks Pale Glaucous-Green; skin between scales on body otherwise black; infralabials and genials nearly white, faintly buffy; throat Cream-Buff; gastrosteges Deep Olive-Buff on posterior and lateral portions, Olive-Buff or Pale Olive-Buff anteriorly; this color intensified to Tea Green on posterior urosteges; skin between gastrosteges black; 12th and following gastrosteges marked with Vinaceous-Rufous blotches, forming nearly continuous red streak down belly;

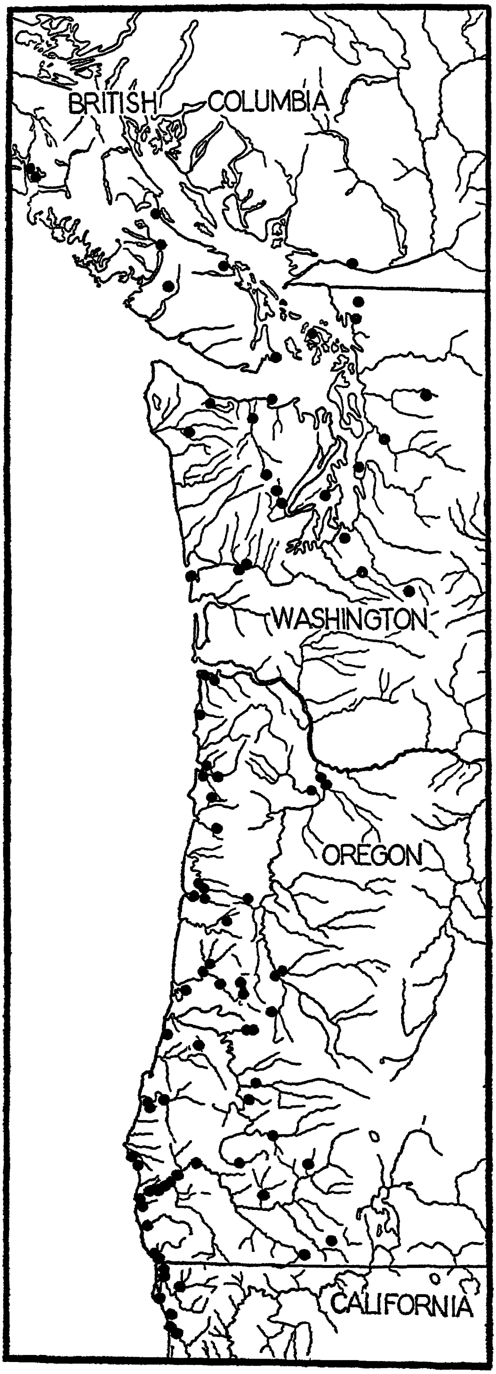

Fig. 17. Range (localities of specimens examined) of *Thamnophis ordinoides ordinoides* in British Columbia, Washington, Oregon, and California; in the last-named state it is restricted to the extreme northwest corner.

this red coloring continuing onto tail, but sparser there—only three small red blotches on its distal third.

Description of freshly killed adult female (Mus. Vert. Zoöl. No. 18994) from Snohomish, Snohomish County, Washington (typical of the northern population of the subspecies).

Top of head Olive-Brown dotted with black; anterior supralabials Tea Green, posterior ones paler, Pale Cendre Green; dorsal stripe between Ochraceous-Orange and Ochraceous-Buff, brighter, nearer Ochraceous-Orange at anterior end; posterior genials and scales between them tinted with Light Ochraceous-Salmon; throat immaculate; anterior gastrosteges Pale Olive-Buff shading into Olive-Gray posteriorly, where increasingly dotted with black; gastrosteges on posterior half of body entirely black.

Comparisons.—*T. o. ordinoides* intergrades with *T. o. atratus*, and its range overlaps without intergradation the ranges of *vagrans*, *elegans*, and *hydrophila*. Comparisons with each of these forms are made under their respective headings.

Remarks on nomenclature and systematics.—In the original description of this form, published in 1852, Baird and Girard mentioned no specimens by catalogue number, but Puget Sound was stated to be the type locality and the description fits the kind of garter snake in that region to which I apply the name *ordinoides*. In 1853 the same authors reapplied the name *ordinoides* to snakes of the subspecies *atratus* from the San Francisco peninsula. In consequence, the name *ordinoides* was long associated erroneously with the California race to which the name *atratus* was later applied. In 1853 Baird and Girard gave the Puget Sound race another name, *leptocephala,* which name was thereafter generally applied to it up to the time of Ruthven's revision in 1908. Meek in 1899 created the synonyms *olympia* and *rubristriata,* both of which color variants from the Olympic Mountains attested to the great variability of this form.

Ruthven (1908 :147) included both *ordinoides* and *atratus* under the name *ordinoides.* Even though he merged the two forms, Ruthven's diagrams of variation in scale characters showed that nearly all series from localities north of Humboldt County, California, were well set off from series from Humboldt County and from more southern parts of the range in lower average numbers of scale rows, gastrosteges, urosteges, supralabials, and infralabials, and in having the preoculars more frequently divided. Ruthven's charts show that series from Vancouver Island and from Puget Sound, though averaging low in numbers of scale rows, gastrosteges, urosteges, and labials, have high maxima, and it seems highly probable that individuals of *vagrans,* which occurs in that region, may have been included. Ruthven (1908 :156) recognized the fact that Californian populations of these snakes differ somewhat in coloration and scalation from populations found farther north, but he objected to dividing them into separate subspecies on the grounds that these differences were slight and inconstant.

Van Denburgh and Slevin (1918) demonstrated that *ordinoides* is well set off from *atratus* in many characters including size, coloration, and scalation, and that the transition between the two forms is abrupt. The present study has indicated that this division was fully justified and that the differences separating *ordinoides* from the other races are much greater than those ordinarily found between subspecies of the same species.

Geographic variation and intergradation.—*T. o. ordinoides* shows but little variation in most scale characters and is well set off from all the other subspecies. The number of preoculars is, however, subject to much variation (see p. 108). In the northern part of the range in British Columbia and the Puget Sound region, the majority of individuals have the preocular divided on one or both sides, but in southern Oregon this scale is nearly always single on each side. Numbers of ventrals seem not to show continuous geographical trends, though series from different localities show local differences which are constant in both sexes. Specimens from the Willamette Valley have on the average more gastrosteges and urosteges than have those from localities nearer to the coast. Series of *ordinoides* from all parts of the range are notably constant in numbers of supralabials and average approximately 7 pairs (see p. 109). Numbers of infralabials are more variable both individually and geographically than are numbers of supralabials, though all series averaged between 8 and 9 pairs (see p. 110). Series from the northern end of the range, from Vancouver Island, and those from the southeastern part of the range in Oregon, average nearer 9 pairs, and those from western Washington and from the Oregon coast average nearer 8 pairs.

In series from Vancouver Island and northwestern Washington and those from the coast of southern Oregon at the opposite end of the range, the scale rows are relatively short; in series from the interior valleys of Oregon these rows are noticeably longer, especially in those from Eugene at the south end of the Willamette Valley (see p. 107).

Coloration is far more variable than scutellation in this form. In specimens from British Columbia, the dorsal stripe is usually dull yellow, somewhat suffused with the brownish ground color, but it may be reddish or orange. In the Puget Sound region, the majority of individuals have a bright yellow dorsal stripe, which is usually narrow, sometimes nearly confined to the mid-dorsal row. The ground color is usually black in such specimens. Some from this region have a red dorsal stripe, as had the type of Meek's *Thamnophis rubristriata* (1899:235) from the Olympic Mountains. In specimens from northwestern Oregon the dorsal stripe is most frequently yellow, but is often orange or red. In series from the Willamette Valley, Oregon, from Benton and Lane counties, the stripe is nearly always bright yellow, but often is streaked with orange. Oregon specimens from eastern Douglas County, and from Jackson County, are likewise nearly all yellow striped. Those from Curry County differ from them in having the dorsal stripe red, though it may be faint and much suffused with the dorsal ground color; sometimes the stripe is hardly discernible, but only rarely distinctly yellow. Such specimens have the ground color brown rather than black, often suffused with greenish or bluish tints; and they may have no lateral stripes. The ventral surface is often extensively marked with red; in extreme instances the entire dorsolateral area may be predominantly red.

In snakes of Del Norte County, California, the red-striped pattern described above is common, but yellow-striped specimens also are of frequent occurrence. Such specimens show affinity with *atratus* rather than with the yellow-striped *ordinoides* farther north, as is attested by the red markings on the sides. In typical *ordinoides* the ventral surface and sides are never marked with red unless the dorsal stripe is of the same color.

To review the variation mentioned above, it may be said that at least three differentiation centers can be distinguished within the range of *ordinoides*. In northwestern Washington this subspecies usually has dark, nearly black, ground color, a narrow dorsal stripe, distinct, pale, lateral stripes, heavy black pigmentation on the ventral surface, divided preoculars, shortened body scale rows, 7 pairs of supralabials, 8 pairs of infralabials, and reduced numbers of gastrosteges and urosteges. Populations from the interior valleys of Oregon west of the Cascade Mountains also have dark ground color, yellow dorsal stripe, and distinct lateral stripes, but they lack extensive pigmentation on the ventral surface, have undivided preoculars, relatively long body-scale rows, relatively great numbers of gastrosteges and urosteges, and 9 rather than 8 pairs of infralabials. Series from the coast of southern Oregon, especially from Curry County, usually have a red dorsal stripe, which may be obscure; dull, indistinct, lateral stripes; a pale greenish or bluish dorsal ground color; a pale immaculate or red-spotted ventral surface; undivided preoculars; relatively short body-scale rows; relatively few gastrosteges, a relatively large number of urosteges, and 9 pairs of infralabials.

Habits and habitat.—In the week from May 20 to May 27, 1935, 80 individuals of *ordinoides* were seen by me in the vicinity of the mouth of Lobster Creek, Rogue River, Curry County, Oregon. Nearly all were on benches of "second bottom" 100 feet or more from the creek in grass, or among low bushes beneath alders. No undisturbed individuals were seen in the water and only one entered the water voluntarily. These snakes did not frequent open beaches and rocks along the edge of the creek and were found near the water only where there were bushes and grass on the banks. Several times when individuals were found in such situations near the water, an opportunity was afforded to compare the escape reactions of *ordinoides* with those of *hydrophila,* which occurred there also. Individuals of *ordinoides* seemed not to depend on the water as a place of escape, even though it was readily accessible; they invariably attempted to hide beneath objects on the ground.

In the late afternoon one was found lying along a stick, part of which projected out over the water. Possibly the snake had been drinking before it was disturbed. When alarmed by movements of the observer, it dropped into the water and swam briskly to shore, a distance of only a few inches. There it was easily captured when it tried to hide among loose rocks.

On another occasion a large *ordinoides* was found lying among rocks 5 feet from the water. It crawled under a boulder and coiled. I overturned the boulder, and as the snake attempted to escape, I drove it toward the water. It crawled jerkily with its head close to the ground, continually turning in different directions, apparently searching for some object beneath which it might hide. It crawled into the water, swam out in the current, and swam against it briskly for a few seconds, maintaining its position several feet from shore. Then it turned back toward the bank. By shaking my foot in front of it I prevented it from landing and drove it back into the water, and again it struck out into the current. This performance was repeated many times, but the snake could not be induced to venture more than 5 feet from shore, nor to stay in the water more than a few seconds without attempting to land. It swam with short jerky movements of its body, holding its head high out of the water. During the five minutes or more that it was chased, it progressed several yards upstream. It displayed positive rheotropism and gained slowly against the current. It could have been captured at any time.

On another occasion one was found on moss-covered rocks 3 feet from the edge of the creek. When first seen it was between me and the creek, but it continued to lie motionless. For an instant I held down the end of its tail with my foot. When released, it crawled rapidly to the edge of the water and hesitated there. I approached and pushed it with my foot. It entered the water, but with seeming reluctance, and swam out about 10 feet; then it began to be swept downstream. It swam against the current and after several seconds returned to the shore within a few inches of the starting point. I threatened it with my foot, attempting to drive it back into the water, but it took the offensive and lunged forward with its mouth open. It struck repeatedly as long as it was molested, and kept its mouth open while coiled as well as when it actually struck. In striking, its movements were hesitant and clumsy, and its blows were not accurately aimed. Obviously its offensive behavior was only bluffing. I teased it with my bare hand and, although occasionally I could feel the prick of its teeth faintly when its open mouth touched my hand, it did not actually bite.

Finally, it again took to the water and, as before, swam out a short distance, struggled against the current, and then returned to the starting point on the bank. In all, it did this six times, each time landing to take the offensive against its persecutor rather than remain in the water more than a few seconds. Its movements became sluggish and it seemed to be tiring. The seventh time that it entered the water, it continued to swim out from the bank even when stones were tossed into the water beyond it. Only after it had been carried downstream about 150 feet by the current did it reach the opposite bank and escape. The stream was moderately swift, though without riffles, and was about 50 feet wide at this place.

The 108 individuals of *ordinoides* for which habitat data are available were all found in the vicinity of dense forests in the humid Transition Life Zone, but mostly in meadows or clearings rather than on the forest floor. The habitat of this subspecies is in a region where surface water is abundant, but apparently the presence of water is not a critical factor in its local distribution, as specimens were usually found away from water. Only a single individual was found in water (a small stagnant pool), and this snake was an intergrade which possibly should be referred to another subspecies (*atratus*). Those forced to swim in running water gave evidence of discomfiture and tried more vigorously to escape from the water than to elude capture. In situations where snakes of the Hydrophila group would have taken to the water and escaped, *ordinoides* was helpless and easily captured; it gave no evidence of possessing an instinctive propensity to escape into the water, or of having any of the aquatic tendencies common to most members of the genus *Thamnophis*. An ecologic necessity to this form is the presence of dense ground cover of vegetation offering concealment. None was found in an exposed situation, such as an open gravelly beach, even when the beach was adjacent to a habitat in which the snakes were extremely abundant.

The short stubby body and reduced numbers of gastrosteges and urosteges in *ordinoides* may be correlated with the dense plant growth in its habitat, which affords support for the snake's body as it crawls between the stems, and makes locomotion easier. In crawling or swimming, *ordinoides* appears to be less elastic in its movements than are garter snakes of other races. Probably this is correlated with the fact that it has fewer gastrosteges and consequently fewer ribs and vertebrae. It is therefore less well adapted for moving on open ground than are the slenderer forms which have more vertebrae and more elastic bodies. Though *ordinoides* appears to be slower and more sluggish than garter snakes of other kinds, it is capable of disappearing with great rapidity when found in its normal surroundings

Blanchard (1923:363) has demonstrated in the genera *Virginia* and *Lampropeltis* that reduction in body size, reduction in numbers of scale rows, tendency toward uniformity in number of scale rows for full length of body, and shortening of head with reduction in number and sizes of head scales are correlated with secretive and burrowing habits. Although *Thamnophis o. ordinoides* is not a burrowing form, it is secretive; the narrow head, small eye, short, blunt muzzle with reduced and variable number of labials and reduced scale rows are probably correlated with these habits.

In probable correlation with its retiring habits and sheltered habitat, *ordinoides* is of docile temperament as compared with the other subspecies. Evidently it depends mainly on concealment and on its repellent secretion to escape from its enemies. Cornered individuals varied in their defense reactions, but never showed the aggressive behavior and readiness to bite that is characteristic of all members of the Hydrophila group. Some coiled with the head concealed when they were disturbed; others made feeble attempts at self-defense by striking hesitantly, but without attempting to bite. However, on one occasion a large individual which was roughly handled when captured bit my hand determinedly and drew blood.

The bright yellow or red dorsal stripe contrasting with the dark dorsal ground color in *ordinoides* is probably of protective value in concealing motion as the snake glides through thick cover. The probable function of this pattern has been discussed under the accounts of *atratus* and *elegans*.

To summarize available feeding data, 48 specimens contained food or were seen feeding in the field, and they had eaten 67 individual animals. Thirty-two, or two-thirds, of these snakes had eaten slugs; 10 (slightly more than one-fifth) had eaten plethodont salamanders (*Aneides ferreus, Plethodon elongatus, P. dunni*), one had eaten a frog (*Rana aurora*). Of the individual animals eaten, 42 (63 per cent) were slugs, 16 (24 per cent) were earthworms, and 8 (12 per cent) were salamanders.

There is no evidence that *ordinoides* forages at night or even in cool, cloudy weather. All that were found foraging were seen on warm, sunny days. Those found in foggy weather were sluggish and inactive, coiled beneath boards or logs. Evidently the secretive animals which *ordinoides* preys upon are found by it in the daytime when they are inactive and in hiding. This is borne out by field observations. One snake was found in the act of pulling a slug from a crevice in a log where it had been concealed. Individual snakes watched in the process of foraging kept their heads close to the ground and moved slowly along extremely circuitous routes, seeming, for the most part, to follow depressions below the general level of the ground surface. They would pause frequently and sometimes would make lateral peering movements with head and neck before resuming motion. However, they seemed to be guided mainly by tactile sense, perhaps by olfactory sense as well. They were especially prone to investigate niches and crannies or to move beneath logs or other objects on the ground.

At Lobster Creek, juvenal frogs (*Rana boylii*) swarmed at the edges of stagnant pools adjoining the second bottom where *ordinoides* was abundant. None of these frogs was found in the numerous stomachs examined of *ordinoides* from that locality. In order to determine whether the frogs were acceptable to the snakes as food, a dead one was dangled at the end of a string in front of a foraging *ordinoides*. The snake, evidently slightly alarmed by the movements, crawled more rapidly. Only after brushing against the frog's body in passing did the snake recognize it as food (evidently by its odor), seize it, and back beneath a boulder. When the boulder was overturned several minutes later, the snake was coiled and had partly swallowed the frog. The garter snakes' failure to utilize this potential food source probably is a result mainly of their instinctive avoidance of areas of open gravel around the pools where the frogs stay, and also to their inability to catch animals as active as these frogs.

The animals eaten by *ordinoides* were almost all forms incapable either of rapid escape or of vigorous self-defense when attacked. It is evident that *ordinoides* preys mainly on slugs, though it also frequently eats earthworms and plethodont salamanders. All the animals eaten were of terrestrial kinds, and with one exception were forms of inactive and secretive habits that are seldom found in the open in the daytime.

Records of occurrence.—Specimens examined, 495, in the Museum of Vertebrate Zoölogy (unless otherwise indicated), from the following localities:

British Columbia. Friendly Cove, Nootka Sound, 1; Tahsis Canal, Nootka Sound, 2; Alberni Valley, 8; Hall's Ranch, 1; Golden Eagle Mine 20 miles south of Alberni, 1; Newcastle Island, Nanaimo, 4 (2[6])[*]; Departure Bay, 2[6]; Union Bay, Bayne Sound, 1[2]; "Vancouver Island," 11 (10[6], 1[3]); Lillooet River Valley, 1[2]; Fraser Valley, 1[3]; Victoria, 1[6]; no locality specified, 1[6].

Washington. *Whatcom County:* Nooksack Bottom, 1; Bellingham, 31. *San Juan County:* 1[2]. *Snohomish County:* Darrington, 1[1]; Snohomish, 3. *Clallam County:* 12 miles south of Port Angeles, Elwha River, 5[5]; East Twin River, 1[5]; Forks, 1[1]. *Jefferson County:* Mount Steele, 2[3]; *King County:* Seattle, 2[4]. *Grays Harbor County:* West Point, 1[3]; Montesano, 3[1]; Melbourne, 11[1]. *Mason County:* Hoodsport, 3[3]; Lake Cushman, 17 (16[3], 1[1]). *Kitsap County:* Port Orchard, 1[1]. *Pierce County:* Eatonville, 1[4]; Tacoma, 1[1]; Mount Rainier, 1[1]; no locality specified, 2[2].

Oregon. *Clatsop County:* Warrenton, 29; Astoria, 9 (8[1], 1[3]); Cannon Beach, 1[3]. *Tillamook County:* Garibaldi, 4[1]; Trask River, 2[1]; Tillamook, 9[1]; Blaine, 1[3]. *Multnomah County:* Portland, 14 (11[1], 3[3]); near Portland, 6[4]; Sellwood, 8[4]; Milwaukie, 9[4]. *Yamhill County:* between Grande Ronde and Dolphe, 1[2]. *Clackamas County:* Tualatin River 6 miles east of Tualatin, 1. *Lincoln County:* Siletz River, 1[1]; Toledo, 35[1]. *Benton County:* between Chitwood and Siletz River, 7[3]; junction of Little Elk and Yaquina rivers, 2[2]; Philomath, 2[2]; Alsea River near Alsea, 3[2]. *Lane County:* junction of Lake and Deadwood creeks, 1[2]; junction of Siuslaw River and Lake Creek, 2[2]; Linslaw, Siuslaw River, 1; Elmira, 1[1]; Veneta, 1; 2 miles south of Veneta, 1; Eugene, 19; McKenzie River near mouth, 1; 2 miles south of Creswell, 1; Siltcoos Lake, 1. *Douglas County:* Drain, 2[1]; 2 miles west of Drain, 1; north fork of Umpqua River, 1[3]; Ash, 1; 8 miles north of Hauser, 1; Roseburg, 1[3]; Cow Creek, 6[2]; Tiller, south fork of Umpqua River, 1. *Coos County:* 3 miles east of Bandon, 1; 5 miles south of Bandon, 1; Myrtle Point, 22. *Curry County:* Port Orford, 14; 10 miles south of Port Orford, 1; Gold Beach, 1[1]; mouth of Lobster Creek, 71; Silver Creek, 10; 7 miles west of Agness, 1; 2 miles west of Agness, 1; 1 mile east of Clay Hill Creek, 1; Two-mile Creek, 1; Hunter Creek, 4; 1 mile south of Pistol River, 3; Winchuck River, 1; Harbor, 17 (16[1]). *Jackson County:* Elk Creek, 1; Evans Creek 13 miles above mouth, 2; 10 miles east of Ashland, 1; Squaw Creek above Squaw Lake, 1.

California. *Del Norte County:* 3 miles north of Smith River, 1; Gasquet, 2[2]; Smith River, 4[1]; Crescent City, 15 (14[1], 1[2]); 1 mile east of Requa, 1; Wilson Creek, 2; Klamath River 4 miles above mouth, 2; Requa, 2[1].

THE ORDINOIDES GROUP

The Ordinoides group includes two wide-ranging subspecies, *ordinoides* and *atratus;* they are distinct from each other in many characters and intergradation between them is abrupt. *T. o. ordinoides* is more remote from the other subspecies than is *atratus,* which connects it with them. The peculiar char-

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[*] Explanation of references: [1] California Academy of Sciences; [2] Museum of Natural History, Stanford University; [3] Museum of Zoölogy, University of Michigan; [4] Collection of L. M. Klauber; [5] Charles R. Conner Museum; [6] Royal Ontario Museum.

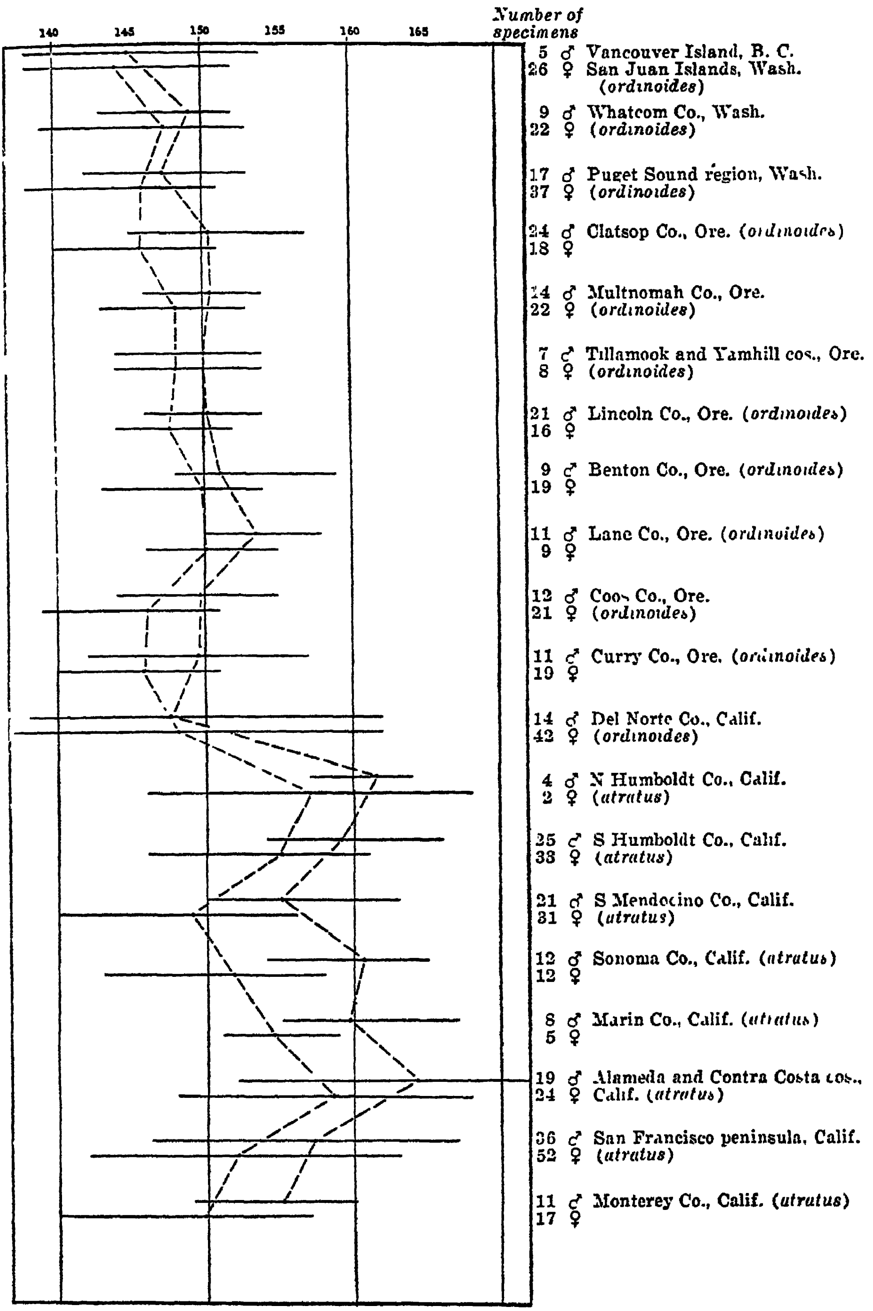

Fig. 18. Numbers of gastrosteges in populations of the Ordinoides group. Note that *atratus* is well set off from *ordinoides* in having more gastrosteges; that the average difference between the sexes is less in *ordinoides* than in *atratus;* that, within each race, more eastern populations (Lane County, Oregon, Alameda and Contra Costa counties, California) have more gastrosteges than do those of the immediate coastal region; that populations of *atratus* differ greatly in average numbers of gastrosteges; that the intergrading population of Del Norte County is highly variable; that *atratus* has maximum numbers of gastrosteges in portions of its range adjacent to the range of *elegans* (Humboldt County).

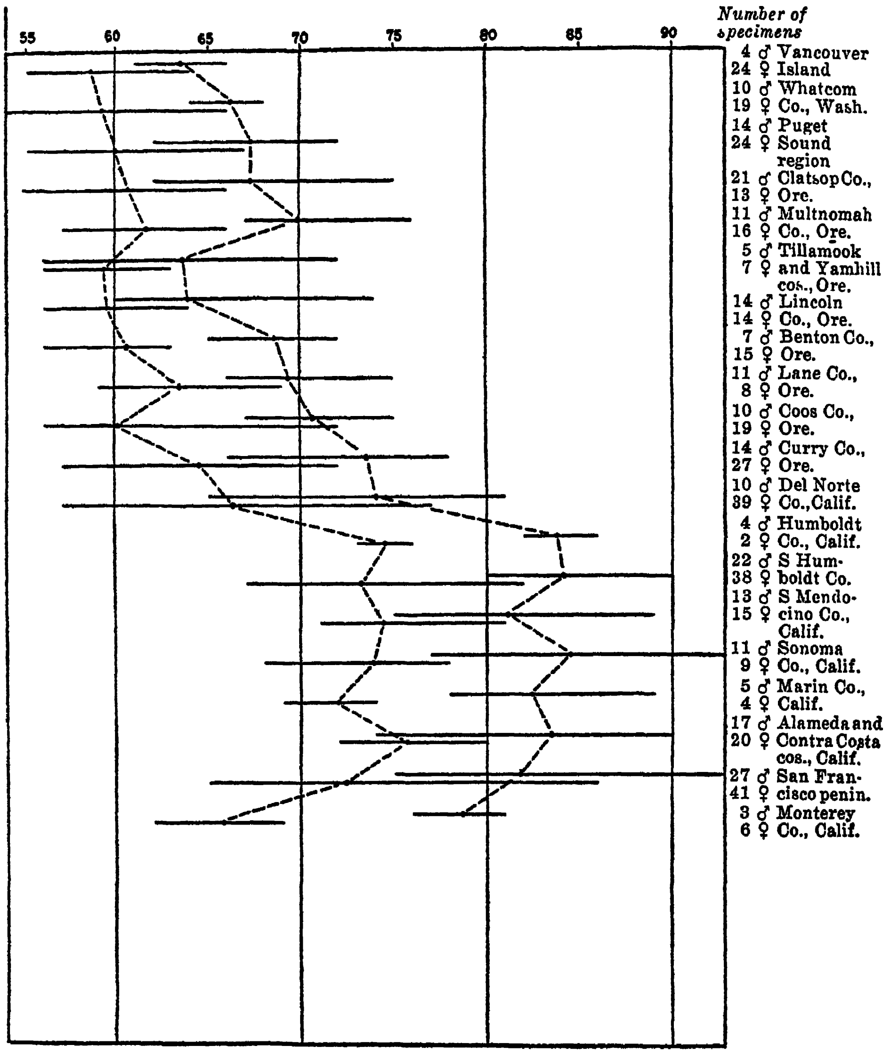

Fig. 19. Numbers of urosteges in populations of the Ordinoides group. Note than *atratus* is well set off from *ordinoides* in higher numbers of urosteges; that the sexual difference is greater in *atratus* than in *ordinoides*; and that geographic trends parallel closely the variation in gastrosteges.

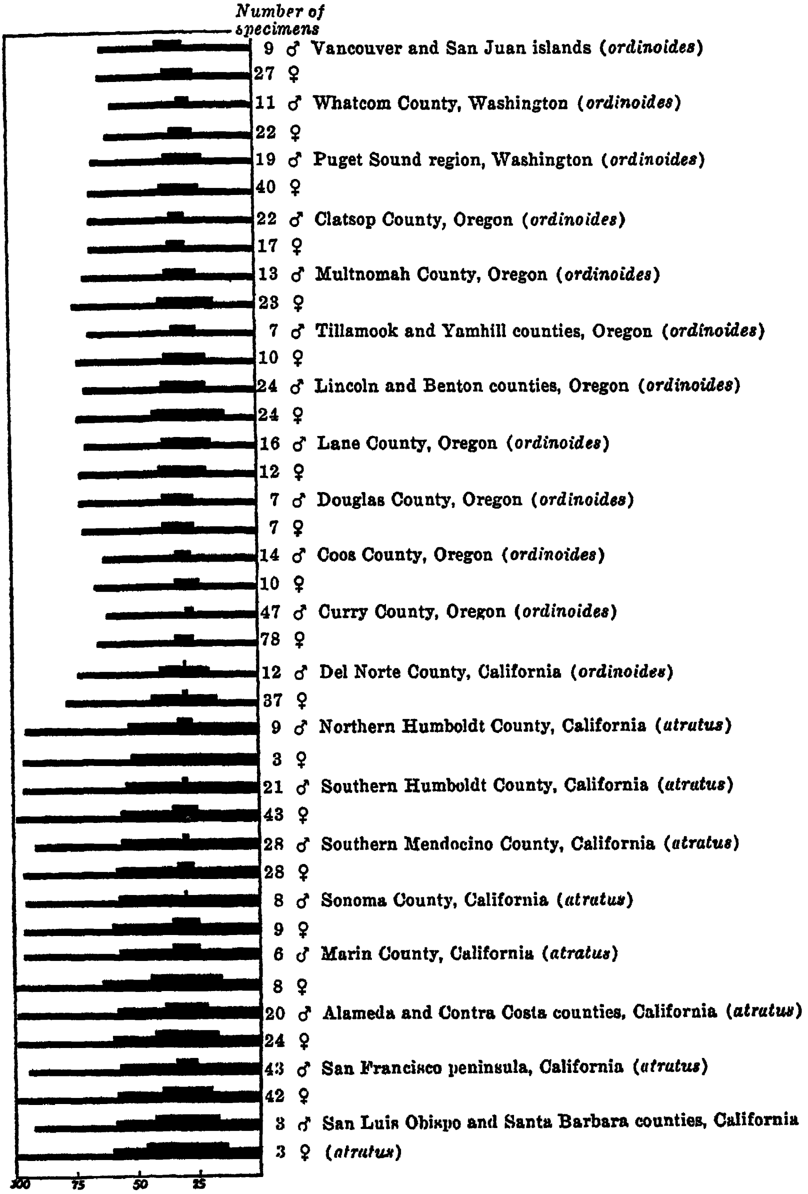

Fig. 20. Diagram showing average lengths and positions of scale rows which vary in the Ordinoides group (plotted for left side of body only). For each series longest (basal) column represents "7th" scale row, the one above it represents "4th" row, and the third or uppermost column, where present, represents "6th" row. Right-hand margin of the figure represents head ends of snakes, and left-hand margin of figure represents posterior ends of bodies. Note that partly suppressed rows center at a point approximately one-third the distance from anterior end of body to anus; that in nearly every series each row averages slightly longer in females than in males; that "5th" row (of the original 23) is lacking in all specimens; that *atratus* is sharply set off from *ordinoides* in having a short "6th" row which is lacking in *ordinoides*; that both forms show local differentiation, the populations nearer the coast having most reduced scale rows, and those from more eastern localities (Lane County, Oregon, Contra Costa and Alameda counties, California) tend to have longer scale rows.

acters of *ordinoides* are in the main merely further developments of the characters which distinguish *atratus* from the subspecies of other groups within the artenkreis.

In both *ordinoides* and *atratus* the head is narrow posteriorly and not distinct from the neck region; the muzzle is short and blunt, the anterior supralabials are short and crowded, or their number is reduced; numbers of gastrosteges, urosteges, and scale rows are reduced. Frequently both have irregular red markings on either the ventral or dorsal surfaces, whereas such markings are not present in snakes of either the Elegans or the Hydrophila group.

TABLE 7

NUMBERS OF PREOCULARS IN POPULATIONS OF THE ORDINOIDES GROUP

Note that preoculars are frequently divided (making a total of 3 or 4) in northern populations of *ordinoides*, but that in southern populations of *ordinoides* and in *atratus* the preoculars are usually undivided (total of 2).

Population	Number of specimens	Number of preoculars		
		2	3	4
Vancouver and San Juan Islands, Wash. (*ordinoides*)	18	.22	.17	.61
Whatcom Co., Wash. (*ordinoides*)	34	.32	.12	.56
Puget Sound region, Wash. (*ordinoides*)	59	.56	.22	.22
Clatsop Co., Ore. (*ordinoides*)	39	.54	.31	.15
Multnomah Co., Ore. (*ordinoides*)	35	.77	.17	.06
Tillamook and Yamhill cos., Ore. (*ordinoides*)	17	.82	.06	.12
Lincoln Co., Ore. (*ordinoides*)	37	.78	.11	.11
Benton Co., Ore. (*ordinoides*)	14	.79	.07	.14
Lane Co., Ore. (*ordinoides*)	30	.90	.03	.07
Douglas Co., Ore. (*ordinoides*)	14	.65	.14	.21
Coos Co., Ore. (*ordinoides*)	25	.76	.20	.04
Curry Co., Ore. (*ordinoides*)	126	.77	.10	.13
Del Norte Co., Calif. (*ordinoides*)	37	.92	.04	.04
Humboldt and Mendocino cos., Calif. (*atratus*)	88	.95	.01	.04
Sonoma and Marin cos., Calif. (*atratus*)	41	.95	—	.05
San Francisco peninsula (*atratus*)	116	.93	.05	.02
Alameda Co., Calif. (*atratus*)	41	.78	.05	.17
Monterey Co., Calif. (*atratus*)	34	.97	.03	—

group.

Both *ordinoides* and *atratus* are essentially terrestrial in habits and seldom enter the water. Both forage typically in dense vegetation in damp situations. Under such conditions probably the pattern is of protective value (see p. 22). The dorsal stripe is usually well defined and brightly colored, red or yellow, contrasting sharply with the dorsal ground color, and the lateral stripes may be conspicuous, also.

T. o. atratus and *ordinoides* are for the most part closely restricted to the humid coastal belt. Though *ordinoides* occurs eastward to the Cascade Mountains, it is confined to a humid climate resembling that of the fog belt along the coast. Data on feeding habits indicate that terrestrial animals are used for food exclusively by *ordinoides* and mainly by *atratus*. Both feed principally on slugs of the genus *Ariolimax*. *T. o. atratus* is, however, more versatile in its feeding habits than is *ordinoides;* on occasion it feeds upon small mammals, birds, or reptiles, or even upon fish. The ranges of *ordinoides* and *atratus* are entirely within the ranges of large coastal forms of *Ariolimax,* which live on rank herbaceous vegetation in moist situations. Probably the presence of these slugs is a critically limiting factor in the distribution of *ordinoides* and *atratus*. Reductions in numbers of supralabials and infralabials in these snakes are evidently correlated with reduction in relative size of head and with secretive habits. Small size of head and reduced numbers of labial scales make for decreased flexibility and extensibility of the jaw, since the scales themselves are somewhat rigid and stretching of the jaw takes place in the loose skin between them. *T. o. ordinoides* is consequently less well adapted to swallow large prey than are the other subspecies. Reductions in numbers of gastrosteges and urosteges, and dwarfing, are probably correlated with the cool climate along the coast where these snakes occur.

TABLE 8

Numbers of Supralabials in the Ordinoides Group

Note that the usual number of these scales in *ordinoides* is 14 (7 pairs), while in *atratus* the usual number is 16 (8 pairs); that populations of *ordinoides* from Del Norte County and of *atratus* from Humboldt and Mendocino counties are intermediate and show complete intergradation in this character.

Population	Number of specimens	Number of supralabials				
		13	14	15	16	17
Vancouver I., B. C. (*ordinoides*)	29	—	.90	.10	—	—
W Wash. (*ordinoides*)	81	.04	.85	.05	.06	—
Clatsop, Multnomah, Tillamook, and Yamhill cos., Ore. (*ordinoides*)	92	.02	.95	.03	—	—
Lincoln, Benton, and Lane cos., Ore. (*ordinoides*)	60	—	.95	.05	—	—
Douglas Co., Ore. (*ordinoides*)	11	—	1.00	—	—	—
Coos Co., Ore. (*ordinoides*)	33	—	1.00	—	—	—
Curry Co., Ore. (*ordinoides*)	83	—	.86	.08	.06	—
Del Norte Co., Calif. (*ordinoides*)	46	—	.59	.11	.30	—
Coast of Humboldt Co., Calif. (*atratus*)	64	—	.31	.17	.52	—
Coast of Mendocino Co., Calif. (*atratus*)	26	—	.26	.07	.67	—
Sonoma Co., Calif. (*atratus*)	30	—	—	.03	.97	—
Marin Co., Calif. (*atratus*)	12	—	—	—	1.00	—
San Francisco peninsula (*atratus*)	118	—	.01	.06	.92	.01
Alameda and Contra Costa cos., Calif. (*atratus*)	41	—	—	.02	.98	—
Monterey Co., Calif. (*atratus*)	21	—	—	—	1.00	—

TABLE 9

NUMBERS OF INFRALABIALS IN THE ORDINOIDES GROUP

Note that the usual number of these scales in *atratus* is 20 (10 pairs), and in *ordinoides* the number is less constant and is nearly always fewer; 18 (9 pairs), 16 (8 pairs), or 17 (9 on one side and 8 on the other).

Population	Number of specimens	Number of infralabials							
		14	15	16	17	18	19	20	21
Vancouver I., B. C. (*ordinoides*)	26	—	.04	.12	.19	.54	.08	.04	—
W Wash. (*ordinoides*)	85	—	.01	.50	.24	.26	—	—	—
Clatsop, Multnomah, Tillamook, and Yamhill cos., Ore. (*ordinoides*)	85	.01	.04	.69	.13	.12	.01	—	—
Lincoln, Benton, and Lane cos., Ore. (*ordinoides*)	58	—	—	.50	.17	.33	—	—	—
Douglas Co., Ore. (*ordinoides*)	10	—	—	.10	.10	.80	—	—	—
Coos Co., Ore. (*ordinoides*)	31	—	.06	.74	.10	.10	—	—	—
Curry Co., Ore. (*ordinoides*)	82	—	—	.34	.13	.43	.06	.04	—
Del Norte Co., Calif. (*ordinoides*)	46	.04	.07	.24	.11	.24	.22	.09	—
Coast of Humboldt Co., Calif. (*atratus*)	67	—	—	.03	.02	.12	.18	.66	—
Coast of Mendocino Co., Calif. (*atratus*)	16	—	—	—	.12	.19	.12	.57	—
Sonoma Co., Calif. (*atratus*)	27	—	—	—	—	.07	.07	.86	—
Marin Co., Calif. (*atratus*)	11	—	—	—	—	.09	—	.91	—
San Francisco peninsula (*atratus*)	118	—	—	—	—	.03	.14	.77	.07
Alameda and Contra Costa cos., Calif. (*atratus*)	39	—	—	—	—	.08	.03	.85	.04
Monterey Co., Calif. (*atratus*)	19	—	—	—	—	.05	.10	.85	—

BEHAVIOR IN CAPTIVITY AND DEFENSE REACTIONS

Behavior of captive reptiles is often a poor indication of their habits under natural conditions; abnormal stimuli bring about abnormal reactions, and normal behavior may be in large part inhibited. Behavioristic studies of caged snakes are therefore to be given little weight as opposed to field observations. Nevertheless, comparisons of different forms under the same laboratory conditions have given clues to differences in habits.

I have kept together adult garter snakes of the subspecies *vagrans, biscutatus, elegans, hydrophila, atratus, ordinoides,* and *couchii.* When food was introduced into the cage containing these snakes, varying reactions were noted in different individuals. When salamanders, *Batrachoseps* and *Ensatina,* were offered, the single individual of *ordinoides* displayed unusual animation, pursuing, catching, and devouring several in rapid succession. *T. o. atratus* and *elegans* also fed readily on the salamanders. Individuals of *biscutatus* seemed indifferent to this kind of food, although the young of one of them, kept in a separate cage, ate several *Batrachoseps.* Although individuals of *vagrans* were attracted each time a disturbed salamander made its characteristic wriggling movements, they did not seem to recognize the salamanders as suitable food; only once was a salamander eaten.

Several large slugs (*Ariolimax columbianus*) placed in the cage were not attacked by any of the snakes despite the fact that under natural conditions *ordinoides, atratus, vagrans,* and *elegans* feed upon slugs extensively, as shown by stomach examinations.

When fence lizards were placed in the cage, *vagrans* at once became active, following them as they climbed along the screen and striking at them when within reach. Often the pursuing snake would miss the lizard and seize another garter snake by mistake and commence to swallow it, so that the attacked snake had to be rescued by the observer. Individuals of *ordinoides* paid no attention to fence lizards when the latter made sudden movements, and never actually attacked them. On several occasions *biscutatus* ate fence lizards, and many individuals of *elegans* fed upon them readily.

A large *T. o. atratus,* kept for several months, quickly caught and ate fence lizards whenever they were offered. On one occasion an adult mouse (*Peromyscus maniculatus*) was placed in a cage with this snake. The mouse climbed about the sides and top of the cage, but the snake followed it persistently, finally caught it by one hind leg, coiled around its body, and constricted it. The mouse's head being free, it bit the snake several times, whereupon the snake merely shifted its coils, continuing to constrict the mouse, which was soon killed and eaten. Once this same snake ate a half-grown alligator lizard.

Individuals of *hydrophila* fed readily upon live *Rana boylii* placed in their cage, and also ate small fish even when these were offered dead.

Garter snakes kept in captivity readily become tame. Among newly caught individuals, however, great differences in temperament may be observed between the subspecies, and between individuals of the same subspecies. All those forms which are aquatic in habits, including members of the Hydrophila group and *vagrans* and *biscutatus* as well, are shy and quick to escape when found in the field, but are pugnacious when caught or cornered. Newly caught individuals of *hydrophila* usually darted to one corner of their cage when disturbed, and flattened their heads and bodies threateningly. Sometimes they would strike even when no disturbing object was within reach. *T. o. elegans* is apparently much less excitable. Although capable of rapid movement when thoroughly alarmed, several of those collected showed perfect equanimity in the field when picked up and handled gently. They made no attempt either to escape or to defend themselves. Occasional individuals of *elegans* will bite when captured.

In all members of the *Thamnophis ordinoides* artenkreis, as in other natricines, the anal scent glands are highly developed, along with an instinctive propensity to use their repellent secretion as a defense against enemies. These glands lie in the base of the tail on either side; they are elongate and extend from the anus distally to a point four or five urosteges behind it. Their ducts discharge a thick, brownish, foul-smelling fluid into the cloaca. When a snake is caught, it may or may not defend itself by striking or struggling to escape, but almost invariably it will discharge its repellent secretion, while it presses the cloacal region against its captor and writhes in such a manner that both its own body and that of its captor become thoroughly smeared.

Although the subspecies vary in their defense and escape reactions, all depend on the protective value of the anal gland secretion. No difference in structure or relative size of the gland could be found among different forms, nor differences in the quality of its secretion or intensity of the odor.

Ordinarily the secretion of the anal glands is not discharged until the snake is caught and held by the pursuer, but this is not invariably so, as is illustrated by the behavior of an individual of *T. o. ordinoides* found in the open crossing a road. It remained motionless as I approached, but jerked back when touched, and made vigorous efforts to escape into bushes at the side of the road. When it was headed off from this retreat, it coiled with its head concealed and performed vigorous writhing movements, drawing its cloacal region along its dorsal surface as it discharged its foul secretion. I have observed similar behavior in *T. sirtalis*. It is improbable that snakes of the Hydrophila group would resort to such means of defense until actually captured, since they characteristically defend themselves by striking when caught in the open. *T. o. ordinoides,* however, is seldom found in the open and less often finds it necessary to fight in self-defense; it seldom does so, even when actually captured.

BREEDING HABITS

Several records are at hand for individuals of *Thamnophis ordinoides* mating in the wild, as follows: March 21, 1936, Berkeley, Alameda County, California (*atratus*); May 2, 1936, Berkeley (*atratus*); March 16, 1936, near Ross, Marin County, California (*atratus*); April 13, 1934, south fork of Cottonwood Creek, Tehama County, California (*hydrophila*); June 26, 1934, Owens River near mouth of Rock Creek, Inyo County, California (*couchii*).

On August 31, 1936, a captive male *hydrophila* showed unmistakable courting reactions toward a female of the same subspecies. Both had been collected about a month before at Trail Creek, Jackson County, Oregon. The female had given birth to a brood of young only four days before the courting behavior was observed. Copulation did not occur.

With the limited data available, no differences can be shown in the breeding habits of the various forms of *Thamnophis ordinoides*. Evidence from gravid female specimens examined indicates that all the races normally breed in the spring during a relatively short season, and that the breeding seasons of the different forms which occur in the same region coincide or at least overlap. Females containing well-developed embryos have been collected only in late summer, and evidently all young are born in July, August, and September. That the breeding season may extend over several weeks in a given locality was indicated by the fact that two large female *biscutatus* of approximately the same size gave birth to broods on August 13, 1934, and September 13, 1934, respectively. Both were collected at the Klamath River near Keno, Klamath County, Oregon, on July 29, 1934, and in captivity were kept together under exactly the same conditions.

Thus, failure of subspecies to interbreed where their ranges overlap cannot well be attributed to different breeding seasons, nor can it be fully explained by habitat differences; individuals of different races have often been found within a few feet of each other, and they must meet frequently in the wild. Failure to interbreed is likewise probably not due to social incompatibility, since these snakes ordinarily show no social behavior, and presumably they have not developed complex instinctive behavior patterns toward one another which might differ sufficiently in different forms to inhibit mating between them. Behaviorisms may be involved, however. I was often impressed with the differing reactions of the less closely related subspecies in the field, and it is possible that more intensive observations would demonstrate differences in the normal behavior patterns of the different forms in all phases of their activity. Comparison of the hemipenis of the different forms disclosed no diagnostic differences; apparently no morphological barriers to crossbreeding exist between any of the subspecies.

The fact that hybrids apparently do not occur in any of the numerous localities of overlapping, in which many possible combinations might occur, is strong evidence that the "barrier" is not one of physiological sterility. In view of the close similarity in external structure, it is unlikely that every race is completely sterile to every other whose range it overlaps, even to the degree of being unable to produce a first generation of sterile hybrid offspring.

The most plausible explanation of the lack of crossbreeding is that differentiation has proceeded so far that snakes of one subspecies do not recognize those of another as suitable mates. If this explanation is to be accepted, it is necessary to assume that the adjustment of the mating reactions is extremely delicate. That the normal mating behavior is easily inhibited is indicated by the fact that it is not seen in caged snakes which otherwise appear hardy in captivity. However, too few individuals were kept under close observation during the breeding season to lend much weight to this idea. Among other groups of vertebrates many examples are known of closely related species of the same genus which, although they occur in the same locality, yet apparently do not interbreed, even when there is no physiological barrier to prevent it.

Obviously, in such situations individual animals, even of forms low in the phylogenetic scale, are able to recognize, and, in respect to mating, discriminate against, members of closely related forms, even when the specific differences are so slight as to be discerned only with difficulty by a human observer. Most of those subspecies of *T. ordinoides* whose ranges overlap are as different from each other, at least in superficial appearance, as they are from the distinct species, *T. sirtalis;* hence it is not surprising that they maintain their distinctness and do not hybridize. Precisely how they are able to discriminate between members of their own subspecies and those of other subspecies is uncertain. It seems probable that skin odors differ in the various forms, especially since their feeding habits differ, and that the snakes readily detect such differences, since they have a well-developed olfactory sense.

COMPARISON OF THAMNOPHIS ORDINOIDES WITH THAMNOPHIS SIRTALIS

Because *Thamnophis ordinoides* shares most of its range with another garter snake, *Thamnophis sirtalis*, which may be a competitor, the ecologic and systematic relationships of these two species are significant. Although Ruthven (1908) placed *T. sirtalis* in a different section of the genus from *T. ordinoides,* there are no scale characters which constantly distinguish them. *T. sirtalis* has only 7 pairs of supralabials, whereas all the forms of the *ordinoides* artenkries, except for the race *ordinoides,* normally have 8 pairs. *T. sirtalis* has a constant formula of body scale rows, 19–17, and in *T. ordinoides* the maximum varies from 23 to 17. The length of the hemipenis constitutes a diagnostic difference between males of the two forms; in *sirtalis* the hemipenis usually extends only to the 8th urostege; in *ordinoides,* to the 14th. In *sirtalis* the dorsal stripe is bright yellow, with a sharply defined line between it and the dark ground color; in some races of *ordinoides* it is suffused with the dull ground color. Even in those which have a bright yellow stripe in sharp contrast with the ground color, close inspection reveals the edges of the stripe to be irregular, blending into the ground color. *T. sirtalis* has red spots on the dorsolateral area, which are mainly confined to the skin between the scales, whereas *T. o. atratus* is the only form of *ordinoides* which has lateral red spots. The spots of *atratus* differ from those of *sirtalis* in that they often invade the lateral stripe, and do not have sharply defined borders. *T. sirtalis* lacks the pale lateral flecks on the dorsolateral area which are present in all forms of the *T. ordinoides* group; also, it lacks the pinkish suffusion of the gastrosteges usually present in races of *ordinoides.* In *T. sirtalis* the eye is relatively larger than in *T. ordinoides*, and the posterior genials are relatively longer than the anterior ones. The foregoing remarks apply particularly to the western races of *sirtalis* which overlap the range of the *ordinoides* complex.

T. sirtalis is less widely distributed in western North America than is the *Thamnophis ordinoides* artenkreis. It is absent from the Lower California peninsula, where two isolated forms of the *T. ordinoides* group occur. Although it overlaps the range of *T. o. vagrans,* it is absent from many of the isolated drainage systems of the Great Basin where *vagrans* occurs. Therefore it seems probable that *sirtalis* is a more recent arrival in western North America than the species *ordinoides,* especially since its races are fewer and less well differentiated. It is evidently more generalized in habitat preferences and feeding habits than are the various races of *ordinoides.*

In the Rogue River basin, Oregon, where three subspecies of *ordinoides* occur together, *sirtalis* is also present. Although it occurs throughout the region, it is, for the most part, abundant only locally where other garter snakes are absent. This may be illustrated by comparing habitat conditions at different localities where garter snakes occur within the region. Along the upper Applegate River, where the stream bed is rocky and the river carries a large volume of swift water the year around, there is but little bottomland or riparian association; the steep slopes are covered with dry woods or with chaparral, and *T. sirtalis* is rare or absent. *T. o. hydrophila* is abundant along the stream; *T. o. elegans* occurs in smaller numbers along the stream and on wooded hillsides as well.

Along the lower course of Trail Creek the stream bed is rocky but the volume of water is small; the current is slow, with still pools; there is bottomland with willows and other riparian growth, and away from the stream there are dry, wooded hills. In this habitat *T. o. hydrophila* is abundant along the stream, *T. o. elegans* occurs in small numbers, and *T. sirtalis* is common. A third ecologic situation exists at Bear Creek, which drains the south arm of the Rogue River valley. The creek goes nearly dry in summer, but stagnant pools always remain. The stream bed is muddy, with sand and gravel in some places. Along the meandering course of the creek there are numerous small sloughs bordered by extensive thickets of willow, blackberry, and nettle. *T. sirtalis* is extremely abundant along some parts of the creek, but I have found no other garter snakes there. In the coastal region of southern Oregon, *T. sirtalis* is abundant though probably less common than *ordinoides*. Thus at Lobster Creek, Curry County, in May, 1935, 11 *sirtalis* were seen, as opposed to 78 *T. o. ordinoides* and 3 *T. o. hydrophila*. One *sirtalis* collected at this locality contained an adult *Dicamptodon*, prey too large to be used by the forms of *ordinoides* occurring there.

Near Eugene, Lane County, Oregon, in June, 1935, *sirtalis* was found in abundance along drying pools of a small creek, where the snakes were feeding upon larvae of *Hyla* and *Triturus*. The water in each pool was muddy from the movements of the snakes, some of which were usually to be seen crawling over the bottom or swimming in the shallow water. Upon being alarmed by the observer, they immediately left the water and darted into thick grass near the pools.

In the Great Valley of California *T. sirtalis* is common along sloughs and slow-moving watercourses. In the coastal region of northern California *sirtalis* is in general less common than either *T. o. hydrophila* or *T. o. atratus*. Whereas *atratus* is sometimes found in chaparral or on wooded slopes, *sirtalis* is usually confined to low ground in the near vicinity of water.

To summarize, *sirtalis* feeds for the most part upon aquatic animals, but apparently is not adapted to securing prey in swift streams; it feeds also upon terrestrial animals, and uses a great variety of prey, including relatively large and active forms as well as small secretive ones; its habitat requirements necessitate the presence of water in slow-moving streams or stagnant pools, and damp meadowland, swampy ground, or thickets of riparian growth in bottomland. *T. sirtalis* is an aggressive species of generalized habits which has been able to find an unoccupied ecologic niche in the region already occupied by the races of *Thamnophis ordinoides.*

ECONOMIC RELATIONS OF SUBSPECIES OF THAMNOPHIS

The data accumulated on the habitats and feeding preferences of the races of western garter snakes suffice to permit an "economic" appraisal of each of the common and widely distributed subspecies. It has not been my purpose to make an economic study, and the economic bearing of my findings is purely incidental in this report. Nevertheless, the subject is perhaps worthy of passing mention here, in view of the widespread popular opinion and extensive popular literature regarding it. It must be emphasized that each form differs from all the others in its economic bearing, and that a general appraisal of any one form might not apply to it at all times and places.

The subspecies *vagrans* utilizes a wide variety of food sources, but most of the animals preyed upon are unimportant to man. Though it feeds extensively on fishes, these are mostly small minnows; I have no definite evidence that it destroys game fishes. *T. o. elegans* likewise does not compete with fishermen, since it is apparently not well adapted to foraging in swift water; most of the fish which it takes are small minnows trapped in drying pools. *T. o. biscutatus* feeds mainly upon aquatic prey, but the fishes which it takes are mostly of small kinds, neutral or harmful from the fisherman's point of view; *Cottus* was the fish most often found in stomachs examined. All three subspecies, *vagrans, elegans,* and *biscutatus,* frequently prey upon toads (*Bufo* and *Scaphiopus*), theoretically of direct benefit to man by reason of their insectivorous food habits; however, rather than to designate the snakes as harmful on this account it probably is more nearly correct to say that they aid in maintaining a natural balance between these amphibians and their biotic associates.

Snakes of the Hydrophila group, *hydrophila, couchii, gigas,* and *hammondii,* commonly called "moccasins," are popularly condemned as destroyers of fish, and are locally believed to be venomous. Because of their reputation as trout destroyers, these snakes, and other garter snakes as well, are usually killed on sight by fishermen. Available data indicate that *couchii* and *hydrophila* do nearly all their foraging among rocks on the bottoms of streams, feeding mainly on fish and tadpoles. Since trout form a considerable proportion of the recorded food, these snakes may be preponderantly "harmful" to the interests of fishermen. However, *hydrophila,* at least, generously compensates for the trout destroyed by eating much larger numbers of the "harmful" *Cottus,* which itself feeds upon the spawn and fry of trout. These snakes may do some damage locally where small trout are concentrated in large numbers, as in rearing ponds; at such places it is recommended that their numbers be kept at a minimum. Under natural conditions, however, they do not seriously reduce the numbers of trout, as is demonstrated by the great abundance of both trout and garter snakes along streams which offer favorable habitat conditions and which have not been fished out by man. The snakes

TABLE 10

RATIO OF INTERNASOROSTRAL CONTACT TO NASOROSTRAL CONTACT

Note the wide range of individual variation, and the distinctness of the Hydrophyla group from the Elegans and Ordinoides groups in relatively narrower internasorostral contact.

Population	Number of specimens	Max.	Min.	Mean
vagrans				
B. C.	12	1.4	.8	1.01
NW Wash.	9	1.2	.8	1.01
Alberta	14	1.2	.9	.99
Mont. and Wyo.	25	1.3	.8	1.02
E Wash.	13	1.4	.9	1.07
Idaho	31	1.4	.8	1.07
Utah	58	1.4	.8	1.07
Nev.	129	1.5	.8	1.08
Col.	49	1.3	.8	1.04
N. M. and Ariz.	25	1.3	.9	1.12
biscutatus				
Klamath Falls	200	1.5	.8	1.09
elegans				
Ash Creek, Calif.	18	1.6	1.0	1.20
Eagle and Grasshopper Lakes, Calif.	24	1.5	1.0	1.18
SW Ore.	13	1.8	1.2	1.35
Sierra Nevada	74	1.7	.9	1.20
Mono County, Calif.	10	1.3	1.0	1.17
San Bernardino Mts.	17	1.3	1.0	1.16
hueyi				
Sierra San Pedro Mártir	14	1.4	.9	1.16
hydrophila				
Rogue River basin	92	1.1	.5	.80
Shasta River basin	15	1.0	.6	.81
Redwood Cr.	18	1.3	.7	.86
Mattole R.	19	1.2	.8	.90
couchii				
Pit R.	9	.8	.6	.67
Upper Sacramento Valley	14	.9	.3	.63
Feather R.	33	.9	.5	.73
Sierra Nevada (E slope)	16	.9	.5	.73
Sierra Nevada (W slope)	32	.9	.4	.74
gigas				
San Joaquin Valley	13	.9	.5	.74

TABLE 10—(*Continued*)

Population	Number of specimens	Max.	Min.	Mean
hammondii				
San Bernardino Mts	29	1.2	.5	.87
San Diego Co., Calif	104	1.6	.6	.94
Sierra San Pedro Mártir	40	1.3	.7	.95
digueti				
Central Lower Calif	34	1.2	.7	.96
atratus				
Alameda Co., Calif	49	1.5	.9	1.14
San Francisco peninsula	53	1.4	.8	1.12
Marin Co., Calif	10	1.3	1.0	1.22
Sonoma Co., Calif	21	1.5	.8	1.14
W Mendocino Co., Calif	19	1.6	1.0	1.24
W Humboldt Co., Calif	77	1.6	1.0	1.23
ordinoides				
Del Norte Co., Calif	14	1.4	1.0	1.19
Curry Co., Ore	43	1.5	.8	1.17
NW Wash	30	1.3	.8	1.04
B. C	14	1.4	.9	1.06

may perform a valuable service in removing dead and diseased fish from the streams. *T. hammondii* feeds mainly on tree toads, and probably its economic bearing is neutral.

T. o. ordinoides feeds almost entirely on large slugs, and, where it occurs, probably constitutes one of the most important natural checks on these eaters of herbaceous vegetation. The great abundance of the snakes about gardens and other places where the slugs may inflict severe damage would recommend them to man as beneficial. The subspecies *atratus* likewise feeds freely upon slugs, so that its economic bearing is similar to that of *ordinoides*. However, it also feeds upon salamanders, small mammals, lizards, and young birds, and so far as it utilizes the lizards and birds, it cannot be considered directly beneficial; possibly it is just the opposite. Rarely it eats fish, but not species important in commerce or sport.

Although it is popularly supposed that garter snakes feed upon insects, and there are general statements to that effect in the literature, no convincing evidence could be obtained from stomach examinations. In several specimens, remains of insects or other arthropods were found in stomachs examined, but the indigestible chitinous fragments appeared to be residual from the alimentary tracts of small vertebrates that the snakes had eaten.

The preceding paragraphs may give the impression that the economic bearing of these snakes is indifferent. However, the artenkreis contains an abundance of widely distributed individuals, and exerts a partial check upon many species of small animals. It is thus important in maintaining a natural balance

TABLE 11

Ratio of Length of Anterior Genials to Length of Posterior Genials

Note wide range of individual variation within each population, and the relatively short anterior genials of *hydrophila*, *hammondii*, and *ordinoides*.

Population	Number of specimens	Max.	Min.	Mean
vagrans				
B. C.	12	.9	.8	.89
NW Wash.	9	1.1	.8	.94
Alberta	14	1.1	.8	.95
Mont. and Wyo.	20	1.0	.8	.87
E Wash.	14	1.1	.7	.87
Utah	25	1.1	.8	.95
Nev.	127	1.1	.6	.83
Col.	13	1.2	.8	.94
N. M. and Ariz.	8	1.3	.8	.94
biscutatus				
Klamath Falls	200	1.1	.7	.84
elegans				
Ash Creek, Calif.	15	1.1	.7	.86
Eagle and Grasshopper lakes, Calif.	26	1.2	.7	.81
SW Ore.	13	1.0	.8	.91
Sierra Nevada	77	1.2	.6	.89
San Bernardino Mts.	17	1.3	.9	1.02
hueyi				
Sierra San Pedro Mártir	14	1.0	.8	.88
hydrophila				
Rogue River basin	94	.9	.6	.75
Shasta River basin	15	.9	.7	.81
Redwood Cr.	18	1.0	.7	.78
Mattole R.	19	.9	.7	.80
couchii				
Pit R.	9	1.0	.8	.96
Upper Sacramento Valley	13	1.0	.7	.89
Feather R.	35	1.1	.8	.88
Sierra Nevada (E slope)	17	.9	.7	.82
Sierra Nevada (W slope)	32	1.0	.7	.80
gigas				
San Joaquin Valley	14	.9	.7	.81
hammondii				
San Bernardino Mts.	29	.9	.7	.76
San Diego Co., Calif.	94	.9	.6	.77
Sierra San Pedro Mártir	51	.9	.7	.77

TABLE 11—(*Continued*)

Population	Number of specimens	Max.	Min.	Mean
digueti				
Central Lower Calif.	34	1.1	.8	.94
atratus				
Alameda Co., Calif.	49	1.2	.7	.86
San Francisco peninsula	53	1.2	.7	.88
Marin Co., Calif.	10	1.0	.7	.87
Sonoma Co., Calif.	20	1.2	.7	.85
W Mendocino Co., Calif.	17	1.1	.7	.91
W Humboldt Co., Calif.	77	1.4	.7	.93
ordinoides				
Del Norte Co., Calif.	13	1.1	.8	.91
Curry Co., Ore.	39	.9	.6	.71
NW Wash.	30	1.0	.7	.76
B. C.	14	.9	.7	.79

in the populations of its animal associates. Even where these snakes occasionally conflict with man's interest, their complete extermination seems inadvisable. The elimination of such a common predator might have unforeseen and serious consequences. The fact that garter snakes prey upon animals

TABLE 12

Number of Degrees in Posteroinferior Angle of 6th Supralabial in Populations of the *Thamnophis ordinoides* Artenkreis

Population	Number of specimens	Max.	Min.	Mean	Stand. dev.	Coeff. of var.
vagrans (Nev.)	26	86	73	79.9 ± .88	4.47	5.60
elegans (Lassen Co., Calif.)	27	83	70	78.0± .64	3.33	4.27
elegans (Truckee R. drainage)	13	86	72	78.8	——	——
biscutatus (Klamath R.)	30	84	68	75.9± .83	4.56	6.10
hueyi (Sierra San Pedro Mártir)	9	93	68	89.7	——	——
hydrophila (SW Ore.)	21	80	61	68.6±1.14	0.52	7.58
hydrophila (Redwood Cr.)	18	79	70	74.9± .87	3.7	4.94
hydrophila (Mattole R.)	15	84	67	74.5	——	——
couchii (Pit R.)	8	69	58	62.8	——	——
couchii (Feather R.)	32	71	59	65.4± .64	3.62	5.53
gigas (San Joaquin Valley)	10	83	61	72.3	——	——
hammondii (San Diego Co., Calif.)	95	77	49	64.1± .68	6.65	10.40
digueti (central Lower Calif.)	34	82	63	72.8± .87	5.08	7.00
atratus (Berkeley, Calif.)	34	92	73	81.0± .82	4.79	5.91
ordinoides (Lobster Cr.)	42	88	64	73.6± .98	6.35	8.63

considered valuable to man, such as worms, toads, lizards, and fish, does not necessarily prove that the snakes are harmful; they may be taking only the natural surplus of the prey.

DISCUSSION

Most of the geographic variation within the artenkreis appears to me to be adaptive; this is contrary to Ruthven's conclusion that evolution in *Thamnophis* has been along orthogenetic lines and nonadaptive. Differences in feeding habits and in habitats seem to be correlated with differences in size and proportions of head and body. These differences in turn are reflected in differences in number, size, and shape of certain scales.

Each of the widely ranging subspecies has developed "subraces," some of which might themselves be considered valid subspecies. The entire group is characterized by racial plasticity, and each population displays peculiarities which distinguish it from all other populations; nevertheless, characters undergo alteration much more rapidly in certain regions, so that transition between subspecific characters is for the most part generally restricted to relatively narrow belts. The various subspecies differ greatly in degree of racial differentiation, *T. o. ordinoides* being the most highly differentiated.

The eleven forms may be grouped into ecologic categories according to their method and place of foraging and the type of food used by them. Members of each group in general resemble each other structurally, but they show varying degrees of progressive modification, probably in adaptation to the particular mode of life which they have adopted.

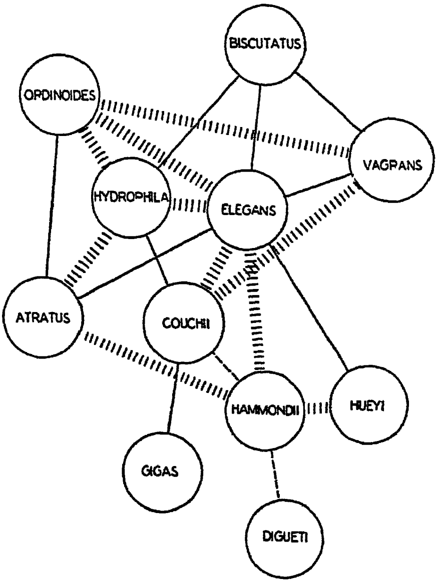

Fig. 21. Diagram showing interrelationships of forms within the *Thamnophis ordinoides* artenkreis. Solid lines represent geographic intergradation; parallel transverse lines represent geographic overlapping; broken lines show affinities where actual intergradation does not occur (between *couchii* and *hammondii*, and between *hammondii* and *digueti*). Note that *biscutatus*, *gigas*, and *digueti* are the only forms which do not overlap other members of the artenkreis.

Evolution within the different groups shows certain parallels or convergences, for example, reduction in size and in number of gastrosteges in the more northern or colder parts of the range. Apparently these trends are determined according to general laws, irrespective of the local habitats or special modes of life. In other characters, such as coloration, pattern, and shape of head, the forms diverge, seemingly in adaptation to special ecologic niches.

Certain characters have no apparent adaptive value, for example, the presence or absence of a horizontal suture dividing the preocular. The forms most remote in other structural characters and in ranges, *ordinoides* and *digueti*, agree in often having the preoculars divided. Ten of the eleven races display this character commonly in some part of their ranges, yet by far the greater number of specimens do not. Since most other species of *Thamnophis* have undivided preoculars, it seems probable that divided preoculars were of frequent or constant occurrence in the common ancestor of the *Thamnophis ordinoides* complex. The fact that this character is of sporadic occurrence throughout the entire group, but is not correlated with any other combination of structural characters nor with habits or habitat, may signify that it is a neutral character in the economy of the species and is not subject to natural selection.

Certain other characters seem to be adaptive in nature, for example, the relatively large size of the supramaxillary glands and the scales covering them in the terrestrial forms *elegans* and *atratus,* and the relatively small size of these glands and the scales covering them in the aquatic subspecies of the Hydrophila group.

Ruthven (1909:408) maintained that . . . . "throughout the genus the germ cells have such a restricted number of potential responses that the different groups have tended to vary in the same direction (homoplasy) under the influence of the environments which have been encountered; that is to say, the similarity of the response is conditioned by the constitution of the animal, the environment only acting as a stimulus upon the germ cells." This statement was made mainly on the basis of variation in size accompanied by changes in numbers of scale rows, ventrals, and labial plates. Ruthven also wrote (1909:403): "It might be assumed (and it would be pure assumption) that this trait [dwarfing] is correlated with unperceived adaptive characters, but this would seemingly be trying harder to save the theory of natural selection than to explain the facts."

That size differences among the races of *Thamnophis ordinoides* are adaptive, now seems obvious from the data at hand about their habits and habitats: A garter snake of the maximum size attained by *T. o. gigas* in the habitat of *T. o. ordinoides* would probably be unsuccessful in finding food of a size and quantity to supply its needs, and it would be hopelessly clumsy in a terrestrial habitat. A snake of the usual size of *ordinoides* in the habitat of *gigas* would be exposed to the attacks of many water birds and other enemies from which the much larger *gigas* is probably immune, and at most times of year it probably would be unable to find animals small enough to feed upon. The largest forms of each group are found in warm climates. The two largest subspecies, *gigas* and *biscutatus,* both occur where there are extensive bodies of water with swamp and marsh conditions. Besides large size, these two forms have in common a stout body and a tendency for the number of scale rows on the body to increase to 23, the maximum number for the genus. These resemblances probably are due to convergence rather than direct relationship, since there are many points of dissimilarity and these forms intergrade indirectly through a relatively small form having only 19 scale rows.

Snakes of such large size and heavy build would be clumsy in an upland habitat. In the water they are not thus handicapped; rather, they are enabled to take advantage of varied food sources, including relatively large aquatic animals which are abundant in their habitat, and perhaps they are safer there from natural enemies than are smaller individuals.

Within each group the smallest adult size is found in the northernmost part of the range or in that part which has the coldest summer climate. Thus, within this artenkreis, and probably within other groups of reptiles, the reverse of Bergmann's Law seems to apply.

On the basis of his theory of orthogenetic evolution, tending to reduction in body size, and in number of gastrosteges, urosteges, scale rows, labials, and preoculars, Ruthven divided the genus into four descent lines. The most primitive form of each line, he found, occurred in the plateau region of northern Mexico, and he assumed this region to be the place of origin of the genus. Forms were found to become progressively more specialized—smaller with reduced scale formulas—the farther they ranged to north or south of this supposed center. He considered *Thamnophis angustirostris* of southern Arizona, southern New Mexico, and northern Mexico to be the ancestral form of his "Elegans Group" (including all the forms of the *ordinoides* artenkreis herein discussed, and a number of less closely related Mexican forms as well). He defined *T. angustirostris* as a large form having 8 or 9 supralabials, 10 or 11 infralabials, 3 pairs of preoculars, 21, or occasionally 23, scale rows, 153–163 gastrosteges, and 65–83 urosteges. Van Denburgh and Slevin (1918: 265) list 18 specimens of *angustirostris* from Arizona, only two of which have more than 8 pairs of supralabials, and none of which has more than 10 pairs of infralabials, nor more than 21 scale rows, but the gastrosteges in their series varied from 161 to 177 and the urosteges varied from 69 to 87.

On the basis of these figures, *angustirostris* is exceeded by *T. o. biscutatus* in number of gastrosteges, urosteges, and scale rows. *T. o. couchii* also exceeds *angustirostris* in number of gastrosteges, urosteges, and supralabials, and equals it in number of scale rows; *vagrans* (in northern Nevada) exceeds it in number of gastrosteges and urosteges; *gigas* exceeds it in number of scale rows. In lacking a dorsal stripe and in having partly suppressed lateral stripes, as well as in frequently having the 5th supralabial separated from the eye by the lowest postocular, *angustirostris* appears to be aberrant rather than primitive; Ruthven himself wrote (1908:120): "In appearance it is one of the most peculiar forms of the genus." *T. angustirostris* also differs from the other forms of the genus in that its posterior maxillary teeth are not conspicuously enlarged. It was placed in a separate genus by Cope on the strength of this character. Since most forms of *Thamnophis,* and even forms of other related genera, agree in having these enlarged teeth, it seems probable that their reduction in *angustirostris* is a secondary, derived character.

According to Ruthven's criteria, it would seem that actually the most primitive forms of *Thamnophis* occur in northern California, northern Nevada, and south-central Oregon. A consideration of all available characters brings the conclusion that *T. o. biscutatus* may be the most primitive form; it is large, has nearly the maximum number of gastrosteges and urosteges (slightly exceeded by *couchii* and *vagrans*), and frequently has 23 scale rows (this maximum number for the genus is not constant in any known form). *T. o. biscutatus* and *T. o. couchii* likewise exceed *megalops, proximus,* and *eques* (the ancestral forms of Ruthven's other three descent lines within the genus) in number of gastrosteges and scale rows, and in body size, and at least equal them in average number of labials. It is evident that either these northern forms are nearest the ancestral stock of the genus, or that the criteria used to indicate primitiveness have been erroneous. The sequence in which the scale rows drop out (see p. 12) seems to preclude the possibility that any form having a given number of scale rows could be derived from a form having a constantly lower formula. However, it seems possible that a form having a given scale row much shortened and vestigial, or even absent in the majority of individuals, might under the influence of natural selection give rise to a form in which the same row is present and extensive.

The forms *T. o. ordinoides* and *T. radix butleri* are dwarfed and have the most reduced scutellation found within the genus. These two forms are also, on the average, the most northern in distribution, though the ranges of certain widely distributed forms extend slightly farther north. As Ruthven demonstrated, all the forms of *Thamnophis* which occur in the United States can be grouped into series, each of which shows progressive decrease from south to north in size and in number of scales.

Small size is probably an advantage to poikilothermal terrestrial animals in a cold climate in that a small body mass makes for rapid adjustment to environmental temperatures. When temperatures become favorably high, the animal quickly recovers from a torpid state and resumes activity. Also, it is easier for a small snake to find shelter, since smaller niches can be utilized.

Since the body surface increases as the square of the linear dimensions, and its bulk as their cube, large garter snakes have a much greater bulk in proportion to surface than do small ones. In an environment in which temperatures during the snake's active season are often much below its threshold of activity, or fluctuate near this threshold, snakes of large bulk would be at a disadvantage, since, being much more slowly warmed to an active condition, they would be in a semidormant and helpless condition much more of the time. If this hypothesis is correct, the cool summer climates of northern regions indirectly cause the dwarfing there.

Likewise, the small size of specimens from the coastal fog belt may be an adjustment to the generally low diurnal summer temperature there, which is frequently below the threshold of activity. Where such climatic conditions prevail, it would be advantageous to be able to adjust rapidly to environmental temperatures and so to utilize brief periods of favorably high temperature in active foraging. *T. o. ordinoides,* the most dwarfed form here considered, is more abundant locally than any of the other forms; it has a wider geographic range and is more generally distributed throughout its range than are most other forms in their respective regions. In view of these facts, I cannot agree with Ruthven in supposing that the environment of *ordinoides* is less favorable to garter snakes than are the environments in which other forms occur. It may, however, be less favorable to *large* garter snakes than to *small* ones.

Of the dwarfed forms of *Thamnophis* which occur south of the supposed center of distribution, all three discussed by Ruthven (*scalaris, phenax,* and *sumichrasti*) evidently are confined to habitats at high elevations in the mountains. All have reduced numbers of scale rows, gastrosteges, and urosteges, as compared with most other forms of the genus. This seems to bear out the supposition that small size as found in these forms, and in *T. o. hueyi,* and in *T. o. vagrans* at the southern end of its range, may be an adaptation to allow rapid adjustment to environmental temperature.

Dwarfing in these southern populations may be an adjustment to the low extremes and great daily range of temperature during the active season at the high altitudes to which all are restricted. In such environments snakes of large size would be slow to recover from the thorough chilling received each night in their temporary shelters near the surface of the ground, and thus would be at a disadvantage as compared with smaller individuals.

Apparently, in the evolution of *Thamnophis ordinoides* the characters most often modified have been body size and number of gastrosteges and urosteges. Characters of coloration and body proportions are more conservative. Probably habits are more stable and more slowly modified than most structural characters; certainly they are less variable in individual snakes.

Within the group, terrestrial habits apparently are correlated with humid climatic conditions and abundant plant growth. Aquatic specialization is probably adaptive to an arid environment, where the snake is forced to seek its food in the water because of the absence of a suitable food supply elsewhere or the impossibility of foraging on open ground (because of high soil temperature). If these assumptions are justified, the wide-ranging ancestral form of the species probably gave rise to the incipient stocks of the Elegans and Hydrophila groups in geographically remote portions of its range under different climatic influences, so that these stocks met and overlapped only after a long period of divergent evolution. After these stocks had differentiated to such a degree that interbreeding did not take place between them when they were again thrown together, their further evolution must have been hastened by the competitive influence which each exerted upon the other. The more terrestrial form, being unable to compete successfully with the more aquatic form in finding aquatic prey, would presumably tend to become further specialized for strictly terrestrial existence; likewise the aquatic form would tend to become more closely restricted to an aquatic ecologic niche in avoiding competition with the more terrestrial form on land.

It is obvious that the complex history of differentiation and migration within this species cannot now be fully traced. Nevertheless, facts at hand concerning the distribution of characters within the group justify certain conclusions about the history of these characters and the development of the forms in which they occur.

T. hammondii and *T. digueti,* the specialized terminal members of the Hydrophila group, obviously are closely related to each other; *digueti* seems to be derived from *hammondii* or from a common ancestral stock closely resembling *hammondii.* The two forms are now separated by an uninhabitable region several hundred miles across in northern Lower California. It seems evident that at some time in the past a more humid climate prevailed in Lower California, permitting migration and perhaps continuous distribution of the ancestral *hammondii-digueti* stock from the northern to the southern part of the peninsula, along a nearly continuous series of river systems, and further, that when such conditions obtained, the Hydrophila group had already diverged from the ancestral *Thamnophis ordinoides* stock almost to its present degree of differentiation.

T. o. hueyi, which is at present confined to the high Transition Life-zone in the Sierra San Pedro Mártir range, is obviously a relict of a formerly more extensive distribution; and it is isolated from the nearest population of the closely related form, *elegans,* in the San Bernardino Mountains, by an uninhabitable territory more than a hundred miles across. The San Bernardino population of *elegans* is likewise apparently separated from the "typical" population on the north by at least a hundred miles in the Tehachapi Mountains region. Therefore it appears that during a former cooler and more humid climatic cycle, when Transition Zone conditions extended continuously from the Sierra Nevada southward into the Sierra San Pedro Mártir, the ancestral *elegans-hueyi* stock had already undergone most of its differentiation from a more primitive form, ancestral to the entire group. Whether the Elegans group and the Hydrophila group invaded the Lower California peninsula in the same cool and humid climatic cycle, or at different times, cannot now be determined. The fact that the Hydrophila group (*digueti*) occurs much farther south at present might be explained by its much greater tolerance for warm climatic conditions.

The same two groups occur farther north, each represented by a form virtually endemic to the Sierra Nevada, both being found throughout that mountain range. It seems probable that both forms have evolved, in part, within their present ranges; that is, they have developed there their present subspecific characters. Meeting and overlapping of the two forms in this region must have been preceded by a long period of isolation and differentiation within separate ranges.

North and west of the Sacramento Valley, the race *elegans* meets and overlaps the most primitive member of the Hydrophila group, *T. o. hydrophila,* to which it bears the same ecologic relation as to *T. o. couchii* in the Sierra Nevada. But where *hydrophila* approaches the range of *biscutatus,* a form closely related to *elegans,* there is rapid transition in characters, and complete intergradation takes place.

The present geographical distribution of primitive characters throughout the range of the species probably is not a reliable indication of the places of origin of the various forms. It is safe to assume that the ancestor of the Hydrophila group had at least 21 scale rows and had a distinct yellow dorsal stripe. At present the distinct dorsal stripe is found within the group only in the population of Trinity County and eastern Mendocino County. The number of its scale rows is reduced to 19 and it is therefore specialized in this respect. Populations of *hydrophila* near the range of *biscutatus* have a dull and faint dorsal stripe. Throughout most of its range the primitively distinct dorsal stripe has secondarily become reduced; it has been retained only in a limited region, which is probably distant from the original home of *hydrophila.*

It is probable that all populations of the group have become somewhat modified from the ancestral forms but in different characters. Hence it is not possible to trace the evolution of the group through the types existing on the present time level, even though they form a nearly continuous intergrading series; forms which appear to be primitive in most respects may be peculiarly specialized in other ways.

In brief, the factors which appear to have controlled the evolution of the group, or artenkreis as here defined, are the following:

(1) *Climate.* Those forms which occur in cool summer climates, whether far to the north, in the coastal fog belt, or at high altitudes, are smaller than their near relatives in warmer climates, and are thereby enabled to undergo more rapid adjustment to environmental temperatures. Size differences between the races are probably adaptive and the result of natural selection, though size is also subject to ontogenetic influences. Numbers of body-scale rows, gastrosteges, and urosteges are closely correlated with size, and genetically small snakes have reduced numbers of scales. In hot arid climates these snakes tend to be aquatic in habits, whereas in cool moist climates they tend to be terrestrial; these tendencies probably are correlated with limitations of physiologic tolerance of the species to heat and cold.

(2) *Habitat.* Aquatic forms tend to be large and thick-bodied, terrestrial forms are usually smaller; those occurring in dry and open situations are slender bodied. Aquatic forms have dull monotone or checkered patterns which are concealing in the exposed streamside habitats; those forms which habitually forage away from the water in dense vegetation have contrasting patterns, with bright longitudinal stripes which conceal motion, and they may have bright red markings.

In the more aquatic forms the supralabial scales behind the eye are small as a result of the relatively small size of the underlying salivary glands. Salivary secretion is less necessary for snakes which feed mainly on streamlined aquatic animals, swallowing their prey under water, than for terrestrial forms. In the latter the posterior supralabials are large and swollen in appearance, covering enlarged salivary glands which presumably supply the needed lubrication for their less easily ingested prey. Snakes which inhabit dense vegetation tend to be secretive in habit. As in other genera of snakes, such habits are correlated with small size, bright markings, relatively small, narrow heads, small eyes, and fusion of labial scales.

(3) *Food supply.* Forms living in arid regions where acceptable food is to be found chiefly in the water have become highly aquatic in habit, with the structural modifications listed above; those occurring in humid regions where

food and shelter are abundant away from the water have tended to become terrestrial in habit, with different instinctive responses in foraging, escaping, and self-defense.

In general, size of each form seems to be proportional (apart from response to climate) to size of prey most available and acceptable to it; thus the smallest form in the group of snakes here considered preys upon worms, salamanders, and slugs, whereas the large forms, *couchii* and *biscutatus,* seek prey of the size of adult toads and fish. Since the larger snakes have more scale rows, this artenkreis seems to provide support for Mell's theory (1929:118) that the number of scale rows is correlated with size of prey; according to this theory, extensibility of the body, and therefore the capacity to swallow large prey, is directly proportional to the number of scale rows.

(4) *Competition.* Forms tending to be aquatic in habits have probably become yet more aquatic as a result of competition arising between them and the more terrestrial forms. The latter, on the other hand, have been forced farther out of the aquatic ecologic niche by the already specialized aquatic subspecies, since nearly every race overlaps one or more races of dissimilar habits.

SUMMARY

The *Thamnophis ordinoides* complex of garter snakes is an artenkreis which includes two isolated species and a rassenkreis of nine intergrading subspecies, all confined to western North America, mainly west of the Great Plains. Most of its forms are confined to the Pacific Coast region. They occur in varied climates under widely differing climatic conditions; they are plastic and adaptable. There is much variation in size, proportions of head, number and length of scale rows, number of gastrosteges and urosteges, size, number, and shape of labial scales, and number of preoculars. Color, intensity, and extent of dorsal and lateral stripes and of other markings, and of ground color, are also highly variable. Most of these characters show geographic trends which are continuous throughout series of forms. The several forms vary greatly in ecologic preferences as well as in structural characters, and these ecologic differences involve the utilization of different habitats and of different food sources.

The entire complex is divisible into three natural groups on the bases of structural characters and ecologic tendencies. Of these, the *Elegans* group is evidently the basic one from which the others are derived; it includes four intergrading forms, *vagrans, biscutatus, elegans,* and *hueyi,* all conservative in characters as compared with members of other groups; all have a distinct yellow dorsal stripe and a broad, flat head, and are either of generalized, partly aquatic habits or are adapted to a dry, terrestrial habitat. The Hydrophila group includes five forms, *hydrophila, couchii, gigas, hammondii,* and *digueti,* the first three intergrading, the last two isolated and differentiated enough to be considered distinct species. All are characterized by medium to very large size, narrow, pointed head, with posterior supralabials and salivary glands reduced in size, dull colors with checkered or monotone patterns, and aquatic habits. The Ordinoides group, including two intergrading forms, *atratus* and *ordinoides,* is characterized by medium or small size, reduced scutellation, bright colors, terrestrial tendencies, and restriction to humid habitats.

Within each of these groups the different forms intergrade where their ranges meet, and replace each other geographically. Also, *biscutatus* of the Elegans group intergrades with *hydrophila* of the Hydrophila group, and *elegans* of the Elegans group intergrades with *atratus* of the Ordinoides group. But in ten other convergences occurring where ranges of forms belonging to different groups meet, there is overlapping without intergradation. Of the eleven forms in the artenkreis, eight overlap the ranges of others. Invariably, ecologic differences between the kinds of snakes involved can be shown. Ecologic divergence relieves competition, so that two or even three subspecies may exist together in the same region. The genetic nature of variation is hence demonstrable; subspecies retain their different and distinctive racial characters even where they occur together under the same environmental conditions in nature. Psychological factors probably are important in preventing crossbreeding between those subspecies which overlap, and discrimination against individuals of another subspecies in mating may be the result of racial differences in skin odors.

Some of the characters which vary geographically are clearly adaptive to environmental conditions. Small size is evidently adaptive to cold climate and small size of prey; a pattern combination of bright yellow stripes on a black background is protective amid dense vegetation, and a checkered pattern of dull colors is concealing in a streamside habitat against a background of gravel. A narrow pointed head is apparently an adaptation for making the snake more streamlined in an aquatic habitat; a broad head is associated with enlarged supralabial glands, supplying the needed lubrication for ingestion of large, rough-skinned, terrestrial prey. Variation and intergradation in ecologic niches paralleling variation and intergradation in structural characters can be traced.

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PLATES

PLATE 1

Fig. 1. Habitat of *Thamnophis ordinoides hueyi* at La Encantada, Sierra San Pedro Mártir; open forest of yellow pine interspersed with granite boulders. *Thamnophis hammondii* also occurs in this region, but is closely restricted to the vicinity of water.

Fig. 2. Habitat of *Thamnophis ordinoides biscutatus* at the Klamath River near Spencer Creek, Klamath County, Oregon; basalt boulders of river edge among which the snakes usually stay.

Fig. 3. Habitat of *Thamnophis ordinoides hydrophila* and *Thamnophis ordinoides ordinoides* at Lobster Creek, Curry County, Oregon. Ecologic separation was apparent here; *hydrophila* was restricted to rocky margins of the stream, while *ordinoides* was extremely abundant in the meadow and beneath alders in middle foreground but did not occur on the open beach.

Fig. 4. Klamath River at same locality as shown in figure 2, showing dry, sparsely forested terrain and rocky margins of river.

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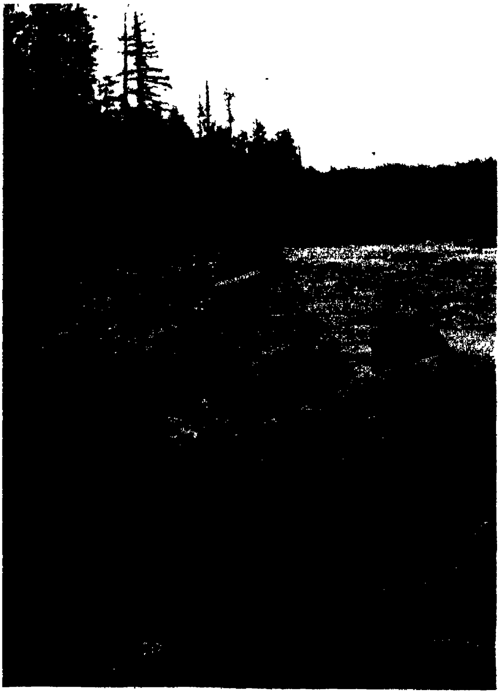

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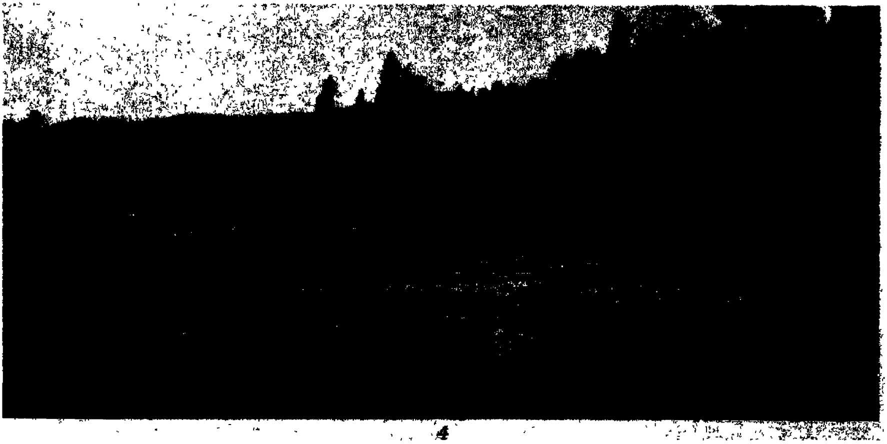

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PLATE 2

Fig 1 Habitat of *Thamnophis ordinoides hydrophila* at Evans Creek, Jackson County, Oregon showing rocks along the edge of the water on which the snakes were usually found

Fig 2 Habitat of *Thamnophis ordinoides elegans* and *Thamnophis ordinoides hydrophila* at Trail Creek Jackson County Oregon *elegans* was uncommon here and was not restricted to the vicinity of the stream, but *hydrophila* was abundant in and around the shallow pools

Fig 3 Habitat of *Thamnophis ordinoides hydrophila* at the Mattole River, Humboldt County, California

Fig 4 Habitat of *Thamnophis ordinoides ordinoides* at Wilson Creek, Del Norte County, California meadow with redwood forest in background

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PLATE 3

Fig. 1. Habitat of *Thamnophis ordinoides hydrophila* and *Thamnophis ordinoides elegans* at the Applegate River, Jackson County, Oregon: *hydrophila* was here restricted to the rocky shore line shown, while *elegans* was found in dry woods on adjacent slopes.

Fig. 2. Habitat of *Thamnophis ordinoides couchii* at Cromberg, Feather River, Plumas County, California. Note similarity to habitat of *hydrophila*.

Fig. 3. Habitat of *Thamnophis ordinoides gigas*, an irrigation canal between Buttonwillow and Tupman, Kern County, California, showing level, arid terrain and riparian vegetation.

Fig. 4. Habitat of *Thamnophis digueti*; dam in creek at San Ignacio, Lower California, showing abundant riparian growth and subtropical aspect of the flora.

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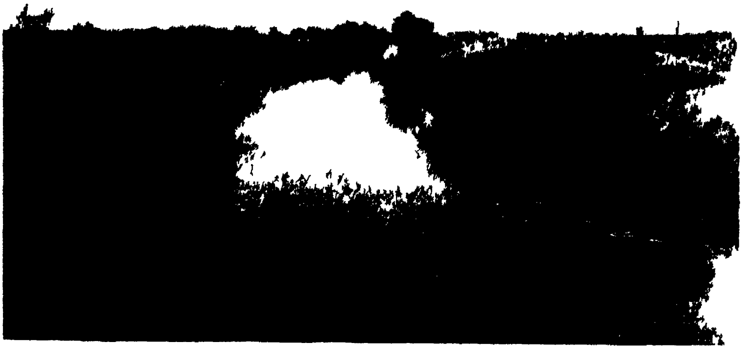

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PLATE 4

Fig. 1. Living adult female *Thamnophis ordinoides elegans* from Applegate River, Jackson County, Oregon.

Fig. 2. Living adult female *Thamnophis ordinoides vagrans* from Deschutes River, Deschutes County, Oregon.

Fig. 3. Living adult female *Thamnophis ordinoides biscutatus* from Klamath River, Klamath County, Oregon.

Fig. 4. Living adult female *Thamnophis ordinoides biscutatus* from same locality as preceding; showing more typical color pattern, with black ground color and bright yellow dorsal stripe.

Fig. 5. Adult female specimen of *Thamnophis ordinoides hueyi* from La Grulla, Lower California.

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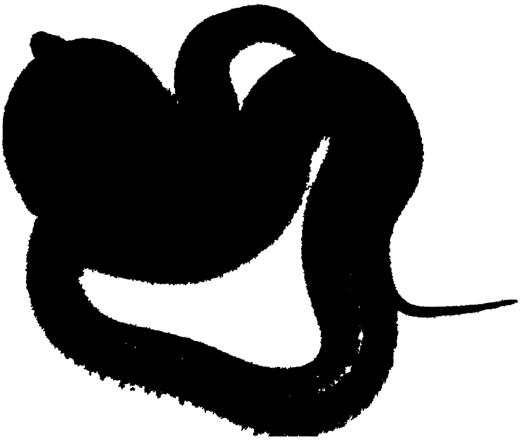

PLATE 5

Fig. 1. *Thamnophis ordinoides ordinoides*, adult female from Klamath, Del Norte County, California, typical of the red-striped southern population.

Fig. 2. *Thamnophis ordinoides couchii* from Yosemite Valley, Mariposa County, California.

Fig. 3. *Thamnophis ordinoides couchii*, living adult female from Feather River, Plumas County, California.

Fig. 4. *Thamnophis digueti.*

Fig. 5. *Thamnophis ordinoides hydrophila*, subadult female of distinctly striped southern population, from Rattlesnake Creek, northeastern Mendocino County, California.

Fig. 6. *Thamnophis ordinoides hydrophila*, subadult male typical of northern population, from Trail Creek, Jackson County, Oregon.

Fig. 7. *Thamnophis ordinoides gigas*, juvenile from near Gustine, Merced County, California.

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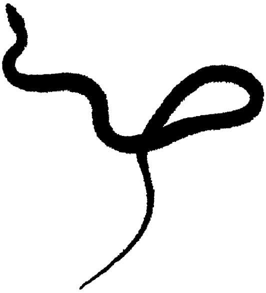

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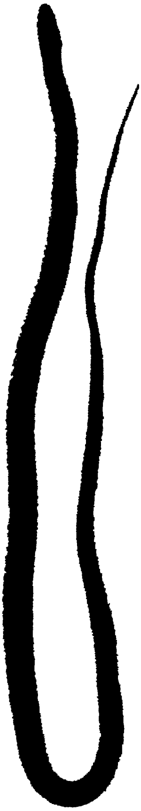

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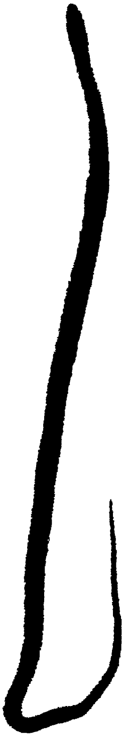

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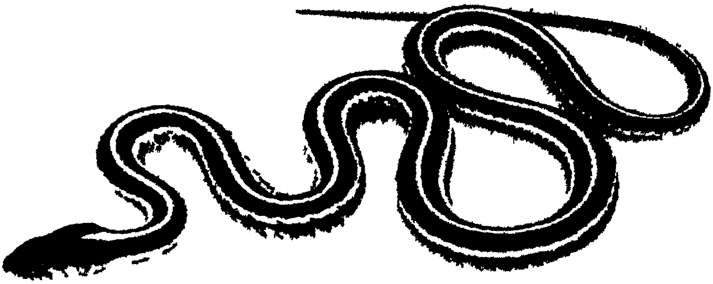
PLATE 6

Fig. 1. *Thamnophis ordinoides elegans*, living adult female from Jackson County, Oregon.

Fig. 2. *Thamnophis ordinoides atratus*, living adult female from Strawberry Canyon, Alameda County, California.

Fig. 3. *Thamnophis ordinoides hydrophila*, living adult male from Trail Creek, Jackson County, Oregon.

Fig. 4. *Thamnophis ordinoides ordinoides*, living adult male from Elk Creek, Jackson County, Oregon.



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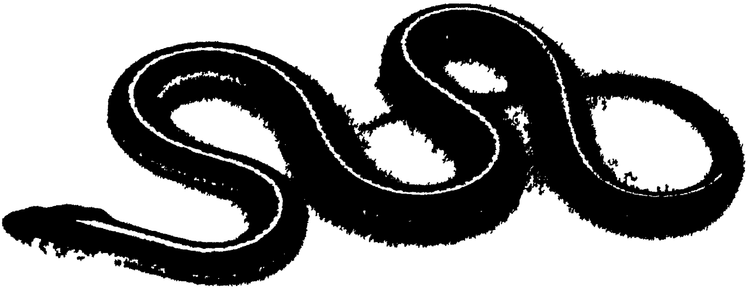

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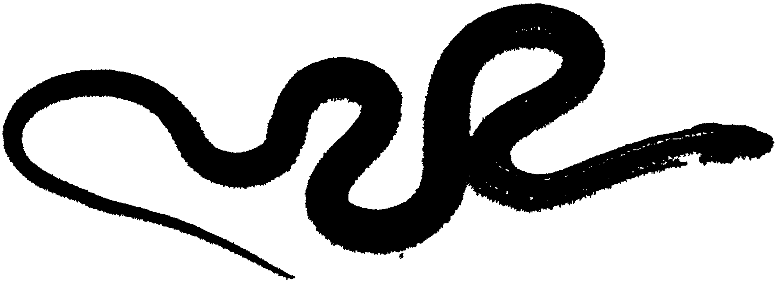

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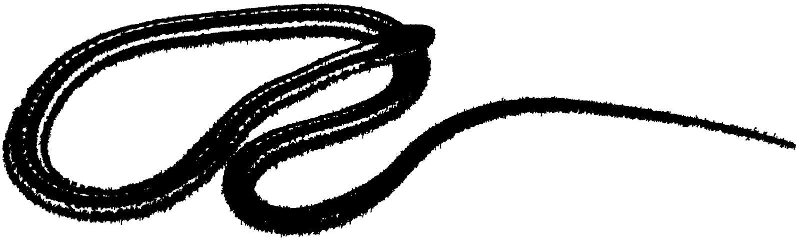

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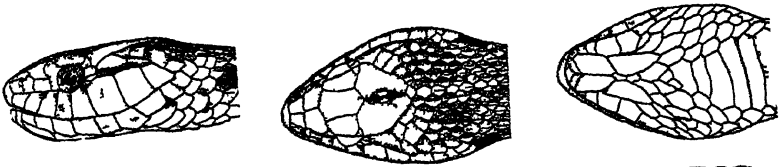
PLATE 7

Heads of *Thamnophis ordinoides* and related species from lateral, dorsal and ventral aspects (1) *T. o. vagrans* (2) *T. o. biscutatus* (3) *T. o. elegans* (4) *T. o. hueyi* (5) *T. o. hydrophila* (6) *T. o. couchii* (7) *T. o. gigas* (8) *T. hammondii* (9) *T. digueti*, (10) *T. o. atratus*, (11) *T. o. ordinoides*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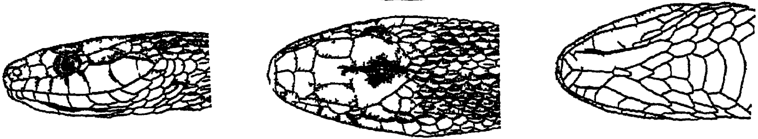
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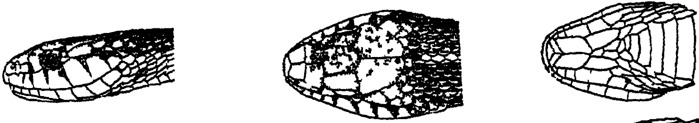
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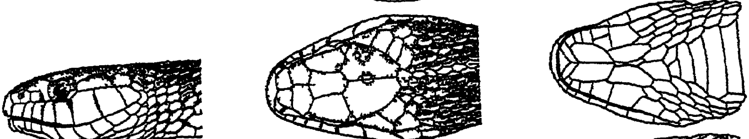
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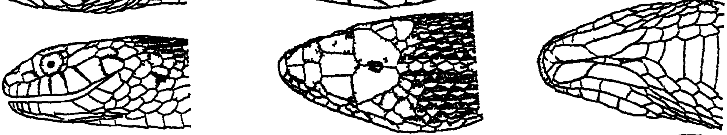
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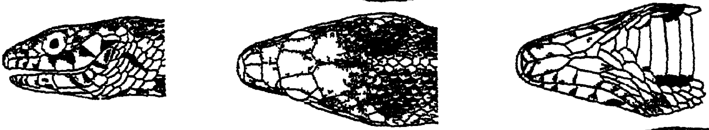
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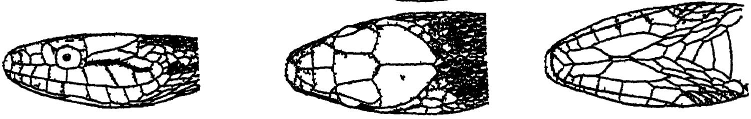
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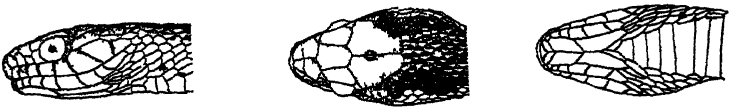
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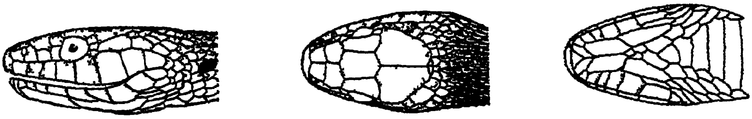
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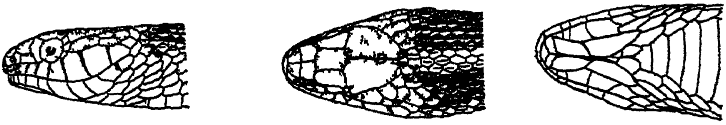
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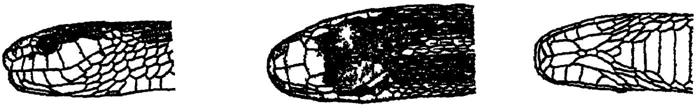
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A FIELD STUDY OF THE GROWTH AND BEHAVIOR OF THE FENCE LIZARD

BY

HENRY S. FITCH

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOÖLOGY
Volume 44, No. 2, pp. 151–172

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY AND LOS ANGELES
1940

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOÖLOGY
EDITORS: J. F. DANIEL, HAROLD KIRBY, S. F. LIGHT, A. H. MILLER
Volume 44, No. 2, pp. 151-172
Submitted by editors June 8, 1938
Issued November 22, 1940
Price, 25 cents

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY, CALIFORNIA

CAMBRIDGE UNIVERSITY PRESS
LONDON, ENGLAND

PRINTED IN THE UNITED STATES OF AMERICA

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BY

HENRY S. FITCH

(Contribution from the University of California Museum of Vertebrate Zoology)

AIM AND METHODS

THE PURPOSE of this field study was to learn as much as possible about the life history of the fence lizard (*Sceloporus occidentalis*) by observing marked individuals over a period of years. The results here reported relate to growth rate of individuals, mating and breeding activities, territorial habits, and rate of replacement in populations. The study of marked lizards was carried on in three separate areas, each of limited extent.

In June, 1933, at Belmont Orchard, six miles south of Medford, Jackson County, Oregon, all the fence lizards were removed from a stretch of rail fence about 150 yards long which passed through an overgrazed pasture, and 18 marked young were released at intervals along the fence to replace them. At the same time an attempt was made to mark and catalogue all fence lizards on a stretch of rail fence about a quarter-mile long in open woods of Garry oak at Dark Hollow, approximately two miles south of Belmont Orchard. For assistance in field work at these two localities I am indebted to members of my family, and especially to my brother, Chester Fitch, Jr. Without his aid my records would have been far less complete, because old and experienced lizards become increasingly wary after repeated captures and the combined efforts of two persons are necessary to hunt them effectively.

In August, 1933, another lot of lizards was marked on their home ground in Strawberry Canyon on the University of California campus near the crest of the Berkeley Hills. These Berkeley lizards lived in a more varied environment than did the Oregon populations. The area was about a quarter-mile long, extending along a board fence and a wooden bridge adjacent to pasture land, eucalyptus trees, Monterey cypress, and native chaparral.

In each of the five years the study was in progress these three areas were visited many times. An attempt was made to mark every individual living on the areas. The first time each lizard was captured it was marked and records were made of its weight and measurements, the date, and the exact place of capture. On each recapture similar data were recorded. Notes on habits were recorded in the field at the time of observation.

By August, 1937, a total of 366 lizards had been marked: 85 at Belmont Orchard; 188 at Dark Hollow; and 93 at Berkeley. Most of the lizards marked were never seen again; only 52 (14.3 per cent) were recaptured the second year, after an intervening season of hibernation; only 9 (2.5 per cent) were taken the third year, after two hibernations; and only 3 (less than 1 per cent) were taken the fourth year. A single individual was taken in five successive years.

Numerous methods of marking were tried. In the season of 1933, lizards were marked by cutting out small patches of scales on the back, or by cutting out the enlarged infralabials of the third row, one on the left side and one on the right in different combinations. In 1934, many lizards were marked by sewing colored threads through the loose skin at the angle of the jaw. This latter method proved unsuccessful, as the threads were eventually lost or faded, although permanent scars remained. In 1935, such of these lizards as were recaptured were again marked by cutting off digits in various combinations; individuals newly caught in 1935 and 1936 were also marked by this method.

In order to obtain data on molting, each lizard was marked with indelible ink at the time of release. Lizards which retained these ink marks until subsequent capture were known not to have molted, whereas loss of the marks indicated at least one molt in the time intervening.

GROWTH

Growth in the fence lizard takes place during three distinct periods. The first, in which the lizard may double its length, is the interval between the time of hatching and the first hibernation. The second, when most of the growth takes place, is the interval between the first and second hibernations. The third, in which the lizard reaches adult size and then apparently stops growing, follows the second hibernation. No growth during hibernation is discernible.

The First Growth Period

In the areas studied, fence lizards hatch from mid-July to mid-September and go into hibernation in mid-November. Thus the earliest hatched would have a growth period about twice as long as the growth period of those hatched latest. The time of hatching and the time of beginning hibernation probably vary from year to year, depending on the weather, and they are affected also, indirectly, by altitude, latitude, and other factors controlling climate. In a given locality the time of hatching may vary according to the nesting site chosen. Also, old females may breed earlier in the spring than younger ones, and their young would hatch correspondingly earlier.

The size of young lizards at the time of hatching was not determined with certainty, because no hatching lizards were found. The smallest lizard which I examined must have been newly hatched. It was caught on September 14, 1937, at Berkeley, and had a head and body length of only 21.5 mm. All other young seen on that date were larger, and some were probably at least a month old. It is probable that most young are larger than this one at the time of hatching, but in all likelihood they are less than 30 mm. in head and body length and weigh less than 1 gram.

Because of the high mortality among the young in the first few weeks of life, the chances of recovering individuals marked at an early age are small. None of the young marked in the first growth period was recaptured in the same period, so that no records of the growth of individuals during that time were obtained. Some indication of the size of the young at the time of entering hibernation was obtained by the recapture, in the spring following hibernation, of individuals marked in the preceding fall. These are recorded in table 1.

It is probable that for the second Berkeley specimen recorded in table 1 the interval between dates of capture almost coincided with the period of hibernation. This 4½-months' interval could have included only a few days of active foraging, and only a little growth is shown; the animal's length increased by about one-fourteenth and its weight by less than one-fifth.

TABLE 1

Specimen	Date	Head and body length (mm.)	Tail length (mm.)	Weight (gm.)
Berkeley, female..........	Sept. 15, 1933	36.5	46.5	1.8
	Mar. 10, 1934	41.0	51.5	2.4
Berkeley, female..........	Nov. 3, 1933	36 0	45.0	1.6
	Mar. 20, 1934	38.0	49.0	1.9
Belmont Orchard, female..	Aug. 2, 1934	29.0	35.0	1.0
	May 15, 1935	51.0	69.0	5.8
Belmont Orchard, female..	Aug. 11, 1933	28.0	35.5	0.8
	April 28, 1934	53.0	67.0	6.8

In contrast to this is the growth shown by the second Belmont Orchard specimen. In a period of 8½ months, including the same hibernation period and, in addition, 4 months of warm fall and spring weather, this lizard grew to nearly twice its first linear dimensions and to more than eight times its first weight. This growth rate is probably unusual, for most of the juveniles taken in April were appreciably smaller. Records of another individual marked at this locality the preceding year show much less growth (table 2).

TABLE 2

Specimen	Date	Head and body length (mm.)	Tail length (mm.)	Weight (gm.)
Belmont Orchard, male....	June 21, 1933	36	46.0	1.5
	July 30, 1933	48	64.5	4.4
	April 28, 1934	54	69.0	7.2

Though approximately a year older than the female recorded in table 1, this male was only 3 mm. longer in total length and 0.4 gm. heavier on April 28, 1934. These two half-grown lizards were then so nearly the same size that one unacquainted with their individual records would as a matter of course assign them to the same age group; yet actually they represent broods of successive years. Most of the growth in *Sceloporus occidentalis* takes place in the first year of life. Hence there is only one well-defined annual age group of immatures at any season; but occasional retarded or accelerated individuals would be wrongly classified by one attempting to assign them to age groups.

Newly hatched young lack the strong predilection for climbing that is characteristic of adults or partly grown young, and they are nearly always to be found on the ground or near it on fallen logs or on rails. An adult usually centers its activity about a bush, stump, tree, or rock outcropping, or some similar place offering adequate concealment, but young are to be found in exposed situations little frequented by adults, such as banks of loose soil, little-used roads or trails, or sand near the edges of streams Evidently these situations are chosen by the female as favorable nesting sites regardless of their suitability as habitats for the young Newly hatched lizards are much less timid than older ones. They attempt to escape pursuers by moving off in any direction rather than making for some definite spot of safety, as an experienced individual does. If hard pressed, one will often try to hide where the shelter is wholly inadequate, thus making itself easy prey.

The young of the year remain active longer in the season than do adults Thus, on November 2, 1933, in Strawberry Canyon, 6 adults and 4 young were seen (about the same proportion as on several previous trips), but on November 10 only 1 adult could be found to 10 young On my next visit to the Canyon, on November 19, no fence lizards could be found although the afternoon was clear and warm. In the first week of November, 1937, near Jamesburg, Monterey County, California, 49 young and only 3 adults were seen. Because of their smaller mass and their tendency to seek shelter in more exposed situations, the young are able to make more rapid adjustments to air temperature, and are sufficiently warmed on sunny days, even in late fall, to emerge from their hiding places and forage, whereas larger individuals in deeper and better-insulated hiding places may remain at temperatures too low to permit their becoming active.

THE SECOND GROWTH PERIOD

In April, after their first hibernation, most of the young have attained a head and body length of between 35 and 45 mm By this time their numbers have become reduced through natural causes, and they are not noticeably more numerous than breeding adults The survivors have become much more wary than they were during the early weeks of life. Each has familiarized itself with its surroundings, forages over a definite and restricted area, retreats to definite hiding places when disturbed, and has definite places of shelter which it occupies at night or during inclement weather.

TABLE 3

Date	Head and body length (mm)	Tail length (mm)	Weight (gm)
May 4	42 5 (38–50)	57 3 (48–68)	3 12 (2 1– 5 3)
Aug. 2	59 5 (55–67)	81 6 (71–88)	8 52 (7 3–11 8)

Individuals a year old often cannot be distinguished in the field from old adults. The rapid growth during the summer following the first hibernation is illustrated by average weights and measurements of 10 young, marked at Dark Hollow May 4 and 5, 1934, and recaptured 90 days later on August 2 and 3. (See table 3, p. 154.)

The gain in size varied in different individuals, irrespective, apparently, of original size, sex, or any other obvious factors. Numbered in order of decreasing size from 1 to 10 on May 4, the young showed on August 2 the following changed sequence when they were again arranged in order from largest to smallest: 2, 1, 7, 5, 3, 9, 8, 4, 6, 10. This example well illustrates the erratic nature of growth, which is evidently controlled, or at least influenced, by factors at present undetermined. Varying food supply at different points along the fence, effects of parasitism, and individual genetic differences may be some of the factors which bring about the observed differences in growth rate in lizards of the same age living in the same locality under apparently similar environmental conditions.

Effect of weather on growth is well shown by measurements and weights of young taken in 1933 compared with those of the series taken in 1934. The winter of 1932–1933 was an unusually severe one, and persistent unseasonably cold weather continued late into the spring of 1933. Plant growth was much retarded, being several weeks behind normal. As shown in table 4, the 1933 brood was about a month behind the 1934 brood in growth during the late spring and early summer.

TABLE 4

Date	Number of young	Head and body length (mm.)	Weight (gm.)
June 6, 1933	25	43.4 (39–47)	3.1 (2.3–4.2)
June 21, 1933	17	43.4 (39–50)	2.8 (1.4–4.3)
May 4, 1934	40	43.0 (37–51)	3.3 (1.8–5.5)
June 23, 1934	20	47.2 (42–53)	4.1 (2.6–5.7)

The June 6, 1933, and June 21, 1933, groups were composed of different individuals; hence the lack of growth during the two-week period may be only apparent. It is probable, however, that actually but little growth took place, since the weather during that time was unfavorable for foraging.

Young may forage with adults, sometimes within a few inches of them, on the same logs, stumps, and rails, but such associations seem temporary and purely fortuitous. The usual attitude of the adults of both sexes toward the young is one of tolerant indifference. Aggressive or threatening behavior by an adult toward a small juvenile is unusual even in the breeding season, when adult males usually display a lively interest in other adults, of either sex, which they happen to meet. One such exceptional incident was witnessed on May 14, 1935, at Dark Hollow, when an adult male was seen to make display movements and to chase off a juvenile which had come to the rail he was occupying. The young are shy and wary of the adults. The earliest recognizable manifestation of territorial instinct was seen in young less than one-fourth grown in the spring after their first hibernation, in April, May, and June.

At this time the young males are already distinguishable from females by their deeper blue ventral patches, and, in those having head and body length in excess of 40 mm., by the bluish or greenish dorsal flecks that are lacking in the females. A young 40-mm. male will dart away when a near-by adult chances to move in its direction, but often will pause to make the characteristic territorial bowing movements with its body vertically flattened to display the bright ventral coloring. The adults involved in these observations gave no indication of noticing the young, whereas similar behavior on the part of another adult probably would have provoked an answering challenge.

Although the young are much less aggressive than adults, small young have been seen to threaten each other on meeting at close quarters. The approached lizard stands high off the ground, tense, with its body vertically flattened and turned sideways toward the other. The second lizard may assume a similar position and both may make bowing movements, less vigorous or sustained than those of adults. One may nip at the other, or actual fights of short duration may occur. Toward the end of summer, as the young approach adult size, they begin to contend with old adults for foraging territory. Territorial pressure is lessened by this time, through the waning of the breeding season and the fighting instincts of the males, and by elimination through natural causes of many of the adults present earlier in the season. On August 4, 1933, at Dark Hollow, a young male 54.5 mm. in head and body length attacked and drove away a large adult male which had been brought from a different part of the fence and released near him. The introduced male fought before retreating, but probably was at a psychological disadvantage because of his recent capture and his release amid strange surroundings.

THE THIRD GROWTH PERIOD

By the spring following their second hibernation, lizards are fully adult and probably comprise a large part of the breeding population. At this age, however, none has attained the maximum size, and most are well under 70 mm. in head and body length. Growth is much slowed down in individuals which have attained the size of breeding adults and may even cease altogether. This slowing down of growth is illustrated (table 5) by a male taken at Berkeley in five consecutive seasons, and already of adult size when first captured.

TABLE 5

Date	Head and body length (mm.)	Weight (gm.)
Aug. 24, 1933	66	12.2
June 15, 1934	68	14 0
Sept. 16, 1934	72	15.1
April 11, 1935	72	14.9
June 21, 1936	72	14.7
April 24, 1937	72	15.6

Another male, already a large adult when first captured, showed slight increase in two successive seasons (table 6).

TABLE 6

Date	Head and body length (mm.)	Weight (gm.)
Aug. 24, 1933	69	13.1
April 1, 1934	71	14.3
June 15, 1934	73	15.5
Sept. 16, 1934	73	16.1
April 11, 1935	73	16.2

MOLT

Adult fence lizards apparently molt by the end of August. At that time they were found either to be in the process of shedding or to have shed recently, as evidenced by the new and glossy appearance of the scales and the loss of the ink marks. Apparently, adults do not molt regularly at other seasons and may undergo but a single annual molt. Several adults marked in August and September and recaptured the following April, May, or June retained the ink marks, and so were known not to have molted in the fall or spring. However, others which seemed to be fully adult (but which may have been newly matured young) have been found molting in October. Numerous adults caught at intervals in the early summer—May, June, and July—did not molt at this time of year, whereas growing young recaptured on the same occasions were usually found to have molted.

The rapid growth of young before the first hibernation, sometimes amounting to twice their original linear dimensions and five times their original weight, seems to indicate that the young undergo several molts before they begin to hibernate, but as no marked young were recaptured in the fall this cannot be demonstrated. A molting juvenile collected in Strawberry Canyon, October 29, 1937, had a head and body length of 34 mm. and a tail length of 43 mm.

During the growing season after the first hibernation, when most of the growth takes place, there are several molts, probably four or five. Data for individual lizards are not full enough to show the usual number, but young recaptured after an interval as long as a month usually had molted. One did not molt between May 4 and July 9, 1934, although in this time it increased 10 mm. in length and nearly doubled in weight. Of 16 young collected from May 14 to May 16, 1935, 11 were in the process of molting, whereas none of the 15 adults captured with them was molting. Three molts is the maximum definitely recorded for any individual during a season, and not more than two molts were actually recorded for most of the young taken several times in the course of a summer. However, the time involved usually represented not much more than half the actual growing season.

REGENERATION OF THE TAIL

Data regarding regeneration of the tail show that growth rate of the new tail varies with the individual. On May 15, 1935, an adult male (twice caught as a juvenile the year before) lacked the end of its tail. The stub of tail that remained was 64 mm. long, almost exactly equal to the head and body length. This individual was recaptured on June 23 and again on July 6, but on these dates no new tail had begun to regenerate.

In an adult male first caught on May 17, 1935, the tail consisted of a 26-mm. regenerated part plus the original basal stub 39 mm. long. When this individual was recaptured on June 23, and again on July 6, the tail had made no further growth. In general the regenerating tail seems to grow rapidly during the first few weeks following a break and when local irritation affords a stimulus, after which its growth slows down and stops. It seems probable that regeneration is more rapid and complete when a break occurs early in life.

TABLE 7

Specimen	Date	Head and body length (mm.)	Tail length (mm.)	Weight (gm.)
Dark Hollow, male........	June 6, 1933	64	59–7	9.7
	May 5, 1934	65	60–9.5	11.1
	June 2, 1934	65	60–9.5	11.3
Dark Hollow, male	May 4, 1934	42	19*	3.1
	June 2, 1934	46	21–4.5	3.8
	July 9, 1934	55	29–23	7.2
	Aug. 2, 1934	60	31–28	8.8
	May 14, 1935	63	33–29.5	8.6
	July 1, 1935	63	33–30	9.2
	July 10, 1936	63	33–30	9.9
Dark Hollow, male	May 5, 1934	46	13*	3.7
	June 3, 1934	51	15–1.5	4.5
	July 9, 1934	56	17–16	6.9
Belmont Orchard, male ..	July 25, 1936	58	54*	8.7
	May 15, 1937	63	61–15	10.1
	Aug. 7, 1937	65	62–16.5	12.3
Berkeley, male............	Aug. 24, 1933	66	49*	12.2
	June 15, 1934	68	53–32	14.0
	Sept. 16, 1934	72	54–13–10	15.1
	April 11, 1935	72	54–13–10	14.9
	June 21, 1936	72	54–13–13	14.7
	April 24, 1937	72	54-13-13.5	15.6

Data on tail regeneration are given in table 7. Measurements of original and regenerated parts are separated by a dash; a second dash indicates that the regenerated tail has itself been broken and a third part grown; an asterisk, that the tail was freshly broken and had not begun to regenerate at the time it was measured.

MATING AND BREEDING ACTIVITIES

Mating activity begins soon after the adults emerge from hibernation in early March. Each male at this time selects some vantage point such as a log, stump, fence post, or boulder, and spends most of his active hours perched conspicuously upon it, keeping watch for insects which may serve as food, and for possible mates or rivals. Adult females are more difficult to find, because they tend to stay nearer the ground and under cover. Apparently, males actually are more abundant. Of 179 adults (arbitrarily including all individuals having a head and body length in excess of 55 mm.) caught on fences where intensive and systematic collecting was done, which should have disclosed every individual, 55.4 per cent were males. Of the 234 young caught, 55.1 per cent were males. Superficial observation on an area where these lizards occur leaves one with the false impression that females are relatively scarce. But close inspection of the vicinity where a male is found often discloses a female at the base of the same boulder or log, perhaps only a few inches from the male. The female seems to be attracted to such a spot within her general sphere of activity by the presence of the male as well as by the favorable nature of the habitat. In the presence of the female the male indulges in frequent courtship displays; he stands high off the ground with his body compressed in a vertical plane, and alternately raises and lowers himself on his front legs in a jerky, rhythmical fashion. The flattening of the body serves to show off the bright blue ventral patches, which are thereby rendered conspicuous in a lateral view, and the jerky up-and-down movements likewise attract attention. The movements take place mainly through flexure of the elbow joint. Each "bow" takes about a second, and usually several are given in succession. If the display lasts more than a few seconds, there are frequent pauses.

Often at the end of a display the amplitude of the bows decreases and their tempo becomes faster, passing into a rapid nodding, as the male, with jerky mechanical steps and quivering muscles, crawls slowly up to the female and flicks her with his tongue or nips at her. The female will not permit such advances unless she is nearly ready to mate; usually she is shy and agile, and will keep out of reach of the males. There are frequent pursuits, and if the female is caught by the male, she struggles, scratches, and bites vigorously, and soon regains her freedom. If the lizards have been basking near each other just before the courtship, the bowing is usually omitted and the male approaches the female while making the nodding movements.

Never was more than one female observed to be in close association with any male. Nor have females been observed to fight among themselves in the wild, or even when kept together in crowded cages. On April 1, 1934, at Berkeley, when a female was transferred to a rock pile occupied by a mated pair, the resident female showed signs of uneasiness, tending to keep between the male and the transferred female, but she made no attempt to attack or drive away the intruder.

In a female recently emerged from hibernation the ova are small and do not noticeably distend the body; later they develop rapidly, giving her a plump appearance. As the time approaches when the eggs are ready to be fertilized, the female becomes more tolerant of the presence of the male. Each member of a mated pair appears to derive satisfaction from the presence of the other, for they are commonly seen basking near each other or in actual contact. Seemingly, the female will permit copulation within a period of only a few days. Actual mating may follow a display by the male, after which he approaches the female, nudges her flanks with his snout, and finally grasps a loose fold of skin on her back behind the shoulder region and to one side. At this stage the female usually struggles and runs, dragging the male after her, but if her struggles are not too vigorous, he retains his hold. After the female stops, there is a pause which may last a minute or more, both lizards remaining motionless except for their heavy breathing and the occasional twitching of their tails. The male becomes brilliantly colored; bluish green areas appear in all his dorsal scales. Then, in a suddent attempt to copulate, he twists his hindquarters beneath the female's tail with vigorous movements. If the female is still indisposed to mate she struggles to escape, and the male's attempt fails. Copulation lasts for only a few seconds.

Wood (1936, p. 177), in describing mating behavior in captive fence lizards, states that the male attempted to turn the female over on her back after having secured a hold, but he did not see actual copulation. Obviously he misinterpreted his observations; Noble and Teale (1930) have shown that when the female lizard is turned on her back the attempt to copulate invariably fails.

I have observed copulation many times in caged fence lizards in March and the early part of April. It was repeatedly noted that females which had mated a few days before displayed a growing intolerance for males. A male courting such a female was repulsed in characteristic fashion; the female would arch its back and make short, jerky hops with head lowered and tail elevated, turning alternately away from and back toward the male, and nipping at him if he did not retreat. The aggressiveness of such females toward males contrasted with the timidity of those which had not yet mated. A gravid female often tolerates the proximity of a male which does not attempt to court her, but seems intensely irritated by any attempt at courtship, and will take the offensive to drive away the male rather than allow herself to be pursued.

Noble and Teale (1930) have described similar behavior in *Sceloporus undulatus*. They state: "In this species the female shows a willingness to mate by hopping around with hunched back and slightly bent limbs." My interpretation of the same behavior in *Sceloporus occidentalis* is exactly the opposite: it shows *unwillingness* of the female to mate. Noble and Bradley (1933, p. 64), describing the same behavior, state: "This performance never seems to stimulate males. It is, however, often provoked by the nearness of a passing male or by an attempt at courtship, but may occur when no males are active. We could secure no evidence that this indicated a willingness on the part of the female to mate. It has nothing to do with ovulation, for eggs were not found in the oviducts of one 'hopping' female which was dissected."

While nongravid females may occasionally show such behavior, it seems to be characteristic of those which have been impregnated, and replaces the instinct to crouch against the ground or to flee, seen in courted females attempting to avoid the attentions of a male before impregnation has occurred. I have frequently seen the hopping reaction in courted females in the wild, and in every instance the female was distended by eggs, and obviously gravid. When gravid females are kept in cages with other fence lizards, where they are subject to frequent annoyance, the hopping gait becomes almost habitual with them in locomotion, and they respond with the hopping reaction to lizards of either sex which approach them. According to my interpretation, the hopping reaction serves to discourage courting males but at the same time advertises the sex of the female and so prevents the male from making a territorial defense against her.

Apparently the eggs are usually deposited late in May or early in June, at least a month after impregnation of the female. On June 2, 1935, at Dark Hollow, a female was found about 200 feet from the point where she was released on May 17, and in the interval she had deposited eggs. Her weight had decreased from 13 to 8.1 gm. Thus, at the time of laying, the eggs seem to have made up more than a third of this female's weight. On June 5, 1928, at the west base of Spencers Butte, Lane County, Oregon, several females were found digging burrows for their eggs in damp soil along a nearly dry creek bed. Evidently they had wandered outside their usual foraging areas for this purpose, since no adult males or juveniles were seen along the creek bed, and an open meadow 100 feet or more across lay between it and the edge of the woods which seemed to provide the nearest permanently favorable fence lizard habitat. These females had balls of mud clinging to their toes. The burrows were made beneath flat rocks in damp soil.

In seven gravid females collected near Berkeley in May and June of different years the number of developing ova varied from 9 to 18, and averaged 13.7. As most adult females breed each year, the reproductive potential is high. After the eggs have been deposited, sexual activity is at an end until the following spring. There is no evidence that a female ever produces more than one brood in a season. Newly hatched young which appear weeks later than the average (e.g., the one recorded on p. 152 taken on September 14) may be the offspring of young females of retarded growth which attained adult size and breeding maturity late in the spring after most of the females had mated.

At Berkeley, where the climate is mild, fence lizards become active earlier in the spring than they do in southwestern Oregon, mating activity beginning soon after they have emerged from hibernation. The eggs are therefore probably fertilized and laid earlier, on the average, in the Berkeley population. However, in at least two different years, a few days after young had been found in moderate numbers at Dark Hollow and Belmont Orchard, they were still rare or absent at Berkeley, apparently having not yet hatched. It would appear that, because of cool summer climate, incubation takes longer at Berkeley than at the Oregon localities.

As the summer passes, the territorial and courting behavior wanes. Males are less likely to be seen perched on conspicuous lookouts commanding views of the surrounding areas, and they less frequently fight or display. Males caught at this time of year can sometimes be kept together in cages without fighting. Courting and fighting behavior may be seen occasionally, however. On August 19, 1935, a male on a tree trunk was seen making vigorous bowing movements, and a female was found a few inches from him. Pairs are to be found throughout the summer resting and feeding in close proximity. In August the nearly full-sized young have thus been found in pairs, the males of which attacked other males released in the vicinity. There is no evidence that these matings are permanent. Individuals seem to form new associations readily with individuals of the opposite sex which they happen to meet, and just as readily relinquish old associations.

TERRITORIAL BEHAVIOR

In the spring each male spends much time at some elevated site within his territory and attacks any adult males which may venture into the vicinity. Hence there is usually but one male to each boulder, stump, or log where conditions are favorable. However, fence lizard territories are not sharply defined or mutually recognized by individuals, as are the territories of some kinds of birds. Seemingly each male defends an indefinite area which centers around his favorite lookout or basking place. This central and desirable position is vigorously defended against intruders. But in peripheral and less familiar areas the male fights with less determination, so that if he happens to wander into the home territory of another individual, he may allow himself to be driven away, even by a smaller and weaker adversary.

There seems to be a gradual shifting of territories as individuals are eliminated and replaced, as the source of food supply changes, or as weaker males are dispossessed of their original territories by stronger ones. At Belmont Orchard, in June, 1933, all adults were removed from the terminal 150 yards of the rail fence and marked young were released to replace them. Two months afterward, in early August, several unmarked adult males (but no adult females) were occupying this part of the fence along with the young. Evidently the lowering of territorial pressure here had permitted an influx of males from farther up the fence where competition was severe. Immigration must have been from this direction, since there was no favorable fence lizard habitat in the open pastures on either side of the fence.

Occasionally, where food and shelter are abundant, two or more males may live in close association, but under such circumstances one seems to assume dominance over the others, as observed in caged *Anolis* by Evans (1935 and 1936). On April 17, in Strawberry Canyon, a large adult male and a female were removed from a pile of eucalyptus logs, and were returned on May 5. On the latter date the weather was warm and clear and fence lizards were active. It was found that the log pile was occupied by four other adult males, and fights were frequent. After releasing the lizards I waited quietly. At short intervals there were sounds of brisk scampering as one male pursued another. These sounds seemed to excite still other males which lay basking on the logs; they raised their heads and looked about alertly, and sometimes one or another of them ran in the direction of the sounds to investigate.

The released lizards sought inconspicuous places in the log pile, and the female was not seen again. The male, however, later became the central figure in a series of fights. It was larger than any of the other males, and also conspiciously marked with ink so that it was recognizable from a distance. In the following account it will be referred to as male No. 1. It was repeatedly attacked by the smaller males. Though not yielding ground readily, it fought apathetically and was not aggressive, merely retaliating when a smaller lizard closed in to bite at it. Probably its fighting ability had been adversely affected by handling and by imprisonment away from sunshine and with insufficient food. Though it was indisposed to take the offensive, the fact that it would not retreat suggested that formerly it had occupied a position of dominance over the smaller lizards in the log pile. Several brief combats between No. 1 and smaller males each ended with the appearance of a third one, attracted by the commotion. The two smaller and more active males would then continue the fight until one chased the other away, allowing No. 1 a temporary respite.

Finally No. 1 moved out on a log extending from the upper end of the pile. It lay there basking in the sunlight, free from disturbance, and several times was seen to feed upon insects. After this period of basking it seemed to feel more at home and became more spirited in its behavior. A male of only slightly smaller size—to be referred to as No. 2—and apparently dominant over the smaller males finally found No. 1 on the projecting log. No. 2 had not been among those which had previously attacked No. 1. Upon sighting the latter from a distance of several feet, it displayed with characteristic bobbing movements, then made a long run up to No. 1 and snapped at it, posing threateningly. No. 1 had assumed a similar threatening pose, and retaliated. In fighting, the lizards crawled jerkily toward each other and snapped at each other's sides, their bodies being greatly compressed in a vertical plane, and their tails elevated. Flattening the body not only showed off to best advantage the brilliant blue of the ventral surface, but also made it difficult for the opponent to secure a hold. During pauses in the fight, bowing movements were performed by one or both. One would renew the attack by closing in to bite at the other's sides or shoulders. Sometimes they would face in opposite directions and bite at each other's flanks. Occasionally one secured a hold and, thus braced, would swing its hindquarters inward by a quick lateral flexure of its back, striking its opponent a sudden blow, usually with such impact that both were sent tumbling. Fighting was almost continual for three-quarters of an hour. During most of this time the two lizards were on the ground beside the log pile, and they circled and milled over an area several yards square. No. 2 was more aggressive than No. 1, usually initiated the attack, and inflicted more punishment, but No. 1 stubbornly refused to yield ground. During much of the fight they were in the open on a trail which passed the log pile. Once, when they were on a log, one seized the other by the hind foot and gave it a sudden flip outward so that both were thrown to the ground. Several times both secured holds simultaneously and then they would roll about on the ground, jerking and wrenching. In frequent brief pauses the combatants faced each other with heads lowered, often with jaws gaping and sides heaving rapidly. After the beginning of the fight, displays were less frequent; the lizards seemed to be using their energies for the struggle.

A curious phase of the combat was the minor part played by the three (or more?) other males which occupied the same log pile. These could usually be recognized individually, one by the skin freshly molted from the top of the head but not from the rest of the body, another by its regenerated tail, and another by its markedly smaller size. Time after time, one or another of these lizards darted out from under cover and joined in the fray for a few seconds, and then scurried back again. Several times, four lizards at once were participating in a free-for-all melee, and often three had holds simultaneously. The two larger lizards for the most part continued to direct their attentions toward each other. Once one of the smaller lizards secured a hold on the shoulder of No. 1 and went through the motions of mating, everting its hemipenes. Meanwhile No. 2 was worrying at both.

In the later stages of the fight both No. 1 and No. 2 showed evidence of fatigue; their attacks became less violent and the intervening pauses were longer. However, they seemed even more absorbed in the fight than before and were less aware of their surroundings, so that I was able to observe them at close range, apparently without their being aware of my presence. The finish came when No. 1, having repeatedly yielded ground in successive clashes, ended a pause, during which he was several inches distant from No. 2, by running across the trail where they had been fighting and into a bush. No. 2 followed immediately, but apparently No. 1 escaped and hid. No. 2 returned to the log pile and basked, but several times ran across the trail to the bush, perhaps having detected slight movements made by No. 1. The latter remained hidden and was not seen again.

On April 7, 1934, several males caught at various places were released at a stone pile in Strawberry Canyon. A resident male attacked them and routed several in rapid succession, some larger than itself. After these one-sided fights had been observed, a second and larger male appeared and, with a surprising show of boldness, attacked a newly released male which I had just dropped in the grass at my feet. The first (smaller) resident male withdrew and apparently hid as soon as the larger one appeared; it was not seen again until the larger male left to pursue an introduced male into thick brush. The smaller male then reappeared and, in the absence of the larger, again dominated the scene, continuing to harass the intruders. Its behavior seemed to show that it recognized the dominance of the larger male in its territory but would not tolerate other intrusions.

As intimated above, dominance seemed to be determined chiefly by size, and where males were found closely associated, the larger seemed to be dominant. When groups of newly caught males were put in cages together, the larger ones often fought persistently, but the smaller ones usually showed no inclination to contest their superiority. Small males generally made themselves inconspicuous by climbing to the top of the cage and flattening themselves against the screen, or by crouching in corners. They were not likely to be molested, whereas any male which displayed was usually attacked by others.

Noble (1934, p. 11) and Noble and Bradley (1933, p. 68) have emphasized the difference between mating behavior and territorial behavior, and the ability of fence lizards (*S. undulatus*) to recognize sex in other individuals. Nevertheless it seems evident that the two types of behavior are closely linked in the psychology of fence lizards. Thus, essentially the same display is used, whether in courting a female or in threatening an intruding male.

At Cottonwood Creek, east of Red Bluff, California, in open blue-oak woods on April 14, 1934, one fence lizard was seen pursuing another, which it finally caught by the tail as they were running along a horizontal branch three feet above the ground. The smaller one struggled and attempted to pull away, dragging the larger lizard after it for several minutes. Finally the larger lizard shifted its hold to the other's side and went through the movements of copulation; one hemipenis was everted, and apparently was inserted into the cloaca of the smaller lizard. The larger lizard then released the smaller, but again pursued it when it ran to escape. The smaller lizard dropped to the ground and hid while the larger stopped and displayed. I caught and examined the smaller lizard and found it to be a male. The larger male watched intently, and when I released the smaller, chased it up an oak tree and continued to follow it for the several minutes that I watched. On numerous other occasions in territorial fights between males in the breeding season, one which has secured a hold on another's side or shoulder has been seen to evert its hemipenis, or to throw its hindquarters beneath the other and, apparently, attempt to copulate. Such behavior may perhaps be best interpreted as indicating that under the stress and excitement of fighting a physiologic state similar to that of mating is attained. Under favorable conditions, when certain movements or positions assumed in fighting happen to resemble those assumed during mating, the characteristic behavior pattern for mating is evoked.

In this connection it is noteworthy that mating normally involves pursuit and struggle. A female physiologically ready to mate struggles only perfunctorily, whereas one at any other stage in the annual breeding cycle resists with such vigor as to repulse the male.

I do not mean to imply that fence lizards cannot distinguish sex. The frequent amicable associations of adults of opposite sex and the lack of such associations between those of the same sex would seem to be sufficient proof of this ability.

The extent to which fence lizards wander seems to vary in accordance with the type of habitat, but evidently shifts in territory are gradual and individuals are reluctant to venture into unfamiliar areas. I found no evidence of homing instinct; lizards (mostly young, but also adults of both sexes) which were transferred a few hundred yards along a fence and released usually settled down in the new locality and never found their way back to their original territories. Just as in the eastern species *S. undulatus* (Noble, 1934, p. 11), females seemed to be even more sedentary and localized in their habits than males. The male cannot be said to have a roving instinct. It is the continual interference from other males competing for territory that makes it more difficult for him to remain permanently in any restricted area. The male caught every year for five consecutive years in Strawberry Canyon lived its whole life, as far as is known, within an area less than 100 feet across. It may have often wandered outside this area without my knowledge.

During 1934 and 1936 this lizard lived in log piles a few yards from the fence and seemingly had optimum habitat conditions for foraging and shelter. In other years the log piles had been removed and this lizard was found along a certain part of the fence. Thus it tended to remain within the same general area but adapted itself to changes in its environment by shifting its headquarters from place to place in order to obtain the optimum habitat available at any one time.

For one of the young marked at Belmont Orchard on June 21, 1933, seven subsequent captures are recorded, in 1934, 1935, and 1936, all along a portion of fence 130 feet in length. This individual was seen and recognized on numerous other occasions, when no record was kept. In the summer of 1934, when two years old (probably having hatched in August, 1932), it was smaller than most adults known to be of approximately the same age. During this season it was almost always seen when the fence was visited. Most of the adults there had become extremely elusive, and upon sighting me at a distance would immediately scurry to safety and hide in some inaccessible place until I had passed. In contrast, the lizard here discussed was surprisingly tame; it often allowed me to approach near enough to catch it by hand, and if such an attempt failed, it would move away a short distance in a peculiarly "nonchalant" manner. Frequently I noosed it before I recognized it, and usually I released it immediately without making records, but always it was in the same general vicinity on the fence. Possibly its peculiar behavior resulted from disease or parasitism.

In 1936 it had grown to nearly the maximum size (length 73 mm., weight 14.8 gm.) and was so shy that it could be caught only twice, each time after long and careful stalking. It was seen frequently during this season, but usually escaped by hiding beneath the bottom rail of the fence in a thicket of rose bushes. Once this lizard was released at the point of capture near one extreme of its known wanderings and later the same day was seen about 120 feet farther down the fence at the other extreme of its known realm of activity, perhaps indicating that this entire section of the fence was within its normal cruising range.

A female marked and released at the end of this fence on August 11, 1933, when it was only 28 mm. long, and probably only a few days old, was captured several times the following summer and again on June 25, 1935. On the latter date, when less than two years old, it was already above the average adult size (length 70 mm., weight 12.4 gm.); its growth had been unusually rapid. In 1934 it had moved up the fence about 120 feet, and there centered its activities around a thick rosebush. Though it was frequently seen, it was extremely shy and much time and energy had to be expended in catching it. On several occasions, when it was cut off from its usual retreat in the rosebush, it was chased for 100 feet or more along the fence.

To summarize similar data relating to the movements of many other individuals (but for each less complete than the records above), it may be said that these lizards are frequently seen on the same log or rail on successive occasions and that in general they are extremely localized in their movements, but that over periods of months or years they may shift their activities over several hundred feet and into new areas. A few individuals were known to have moved for distances of as much as 150 to 200 yards along the rail fences.

The continuously favorable and uniform habitat along the fence may favor exploration and invasion of new territory, and lizards situated on the fence are apt to remain on it in their wanderings. This was true especially at Belmont Orchard, where the fence crossed a heavily overgrazed pasture and there was little cover of the sort required by the lizards except as provided by the fence. Along it at irregular intervals large rosebushes had grown up around the rails, affording shade and thorny protection for the lizards and also probably attracting insects of kinds acceptable to them as food. Clumps of these bushes also grew in the pasture away from the fence, but these apparently did not fulfill the habitat requirements of the lizards, which were seldom seen near them. Apparently an ecologic necessity to this kind of lizard is the presence of something to climb upon—rough, inclined surfaces of wood or rock.

At Dark Hollow the fence passes through an open woods of Garry oak, and lizards occur on logs, stumps, and tree trunks, as well as on the rails. In the late summer of each year most of the lizards which had been present on the fence in April and May were no longer to be found there; apparently they had deserted the fence in favor of adjacent oak trees. In spring and early summer the fence probably provided access to the most favorable forage because insects were abundant in the grass along it. Later in the season, when the grass was dry, and trampled by horses and cattle, the oak trees were more attractive, with their numerous bark- and foliage-inhabiting insects. This tendency of the lizards at Dark Hollow to wander away from the fence made it more difficult to trace individual careers than on the shorter fence at Belmont Orchard.

REPLACEMENT IN POPULATIONS

The original group of 36 lizards marked at Dark Hollow in the first week of June, 1933, was thought to comprise nearly the entire population then occupying the section of the fence (slightly more than a quarter-mile long) where these studies were being carried on. There were 15 young and 21 adults in this original group. In May, 1934, 52 lizards were found on the fence, but 40 of these were small young hatched after the completion of marking operations for the first season. Of the 12 adults 6 belong to the original 36. Thus in less than a year 83 per cent of the original population had been replaced, leaving the number of adults notably reduced. It is possible that the method of marking used the first year caused the death of some. In May, 1935, 49 lizards were found along the fence, and of the 19 adults 8 were survivors of the group marked in 1934. Thus, 43 of the 52 present in 1934, more than

80 per cent of the total, had disappeared and had been replaced. In 1936 the fence was not examined until July. In May, 1937, 45 lizards were found on the fence (and probably a few others were there which escaped capture); 23 were adults, and 9 of these were marked survivors of the 1936 and 1935 groups. Eighty per cent of the population in 1937 thus consisted of newcomers which had replaced those of the year before.

At Dark Hollow, in May of each of these four years, the percentages of small young to the total population were, respectively, 42, 77, 61, and 51. It is possible that the relatively small number of young on the fence the first season may have been a result of high mortality among them during the preceding winter, that of 1932–33, which was unusually severe.

On my trips to these areas and to other localities where fence lizards were abundant, I usually kept records of all young and adults seen. The ratios of young to the whole population, combined for the five-year period and grouped by months, are shown in table 8.

TABLE 8

Month	Total number	Percentage of young
February	8	50
March	74	31
April	113	38
May	196	53
June	52	39
July	20	65
August	135	21
September	156	46
October	170	59
November	73	86

Year-old young recorded in August and September are grouped with adults, since they often cannot be distinguished in the field. It seems evident that these data do not afford a clear picture of the usual relative abundance of young and adults, being distorted by various factors. Actually, young must be more abundant in September than at any other time, all or nearly all the annual brood having hatched by then. Throughout the following year numbers of both young and adults are continually being reduced by natural causes, but presumably the inexperienced young are most rapidly eliminated. In late July and early August, when the young have reached nearly adult size, the population is replenished by a new brood.

Because of their small size, scattered distribution away from the usual habitats, and proclivity for remaining on the ground in inconspicuous places, the newly hatched young are individually much less likely to be seen than the adults. Probably a much smaller proportion of the young than of the adults actually present in an area are seen. To a lesser degree the same probably applies to larger young. In the spring, especially, the adults are readily found because they bask in conspicuous places.

It seems likely that at all times of year young normally outnumber adults. In late summer and fall the recently matured young seem to comprise the majority of the adults.

The rapid rate of replacement of individuals suggests that the life expectancy of fence lizards is short. The adults present during one season will have been largely replaced the following year by young. The individual captured in five successive years in Strawberry Canyon was probably already two years old when first caught in August, 1933, since it was larger than average-sized adults at that time. It must have been nearly six years old when last seen on April 24, 1937. Attainment of this potential life span may be fairly common, but undoubtedly the average is much shorter.

No information on causes of death among the marked lizards was obtained, except for one adult female found dead beside a log pile in Strawberry Canyon on February 24, 1935. This lizard had evidently been hiding beneath loose bark of a log, and had been crushed when the log became dislodged and rolled to the ground. Such accidental deaths may be common, especially in the season of hibernation, but most of the lizards probably become victims of predators, since they are acceptable as food to many kinds of carnivorous reptiles, birds, and mammals.

It might be supposed that adults which have attained a certain age have become seasoned by experience and thus are more likely to survive. However, many of the hazards run by fence lizards seem to be of sorts not readily avoided as a result of individual experience, as, for example, those of the hibernation period. The many predators which catch fence lizards differ greatly in their methods of hunting, and experience in escaping one kind would be of little or no advantage in coping with another. Individuals which I found most difficult to noose did not survive longer, on the average, than tamer individuals.

One of the most destructive enemies of the fence lizard is probably the yellow-bellied racer (*Coluber constrictor mormon*). It was common in all three of the areas studied. I have often seen these racers climbing in low trees and bushes, and even on the rail fences occupied by lizards, though more often they are to be found in grass on the ground. Yellow-bellied racers kept in a large outdoor cage seemed to prefer fence lizards to other kinds of food and were so quick in their movements that they often caught lizards running in the open. In escaping, the lizards usually darted to a place of concealment and crouched motionless. The racers were unable to detect a lizard as long as it did not move. A fence lizard caught by a racer would sometimes turn and bite its attacker, but gradually its hold would loosen and break as the snake worked its jaws forward, and it would then be swallowed without offering further resistance. Rattlesnakes (*Crotalus viridis oreganus*) were present both at Strawberry Canyon and at Dark Hollow. A juvenile rattlesnake collected near Brownsboro, Jackson County, Oregon, in July, 1936, had eaten a young fence lizard. Coral king snakes (*Lampropeltis zonata*) occurred, though not abundantly, at the Oregon localities where studies were made. One contained the tail of an adult fence lizard, and another disgorged eggshells which probably were those of *Sceloporus*. Captive king snakes fed readily upon fence lizards and were able to find them by scent as well as by sight. Other snakes which occasionally prey upon fence lizards are *Thamnophis ordinoides elegans* (at Dark Hollow), *Thamnophis ordinoides atratus* (at Berkeley), *Pituophis catenifer* (at all three localities), and *Lampropeltis getulus californiae* (at Berkeley). Among the avian enemies of fence lizards are sparrow hawks, which foraged regularly over each of the areas studied.

On one occasion when a brown towhee alighted on a fence near a lizard, the latter showed indifference to the bird's presence. The lizard had been chased along the fence for 80 feet, and was watching me keenly as I stood about 20 feet away awaiting an opportunity to maneuver to a more favorable position. The towhee flew up to a rail within a foot of the lizard and perched in full view for at least a minute, turning about and jerking its tail at brief intervals. The lizard continued to watch me and showed no evidence of noticing the bird. This behavior seemed to indicate some intelligence and power of discrimination on the part of the lizard.

It is probable that fence lizards are acceptable as food to most small mammals of predatory or omnivorous habits. Several lizards which at different times were placed in a cage with a grasshopper mouse (*Onychomys torridus*) defended themselves spiritedly, their aggressive behavior contrasting sharply with the quiescence of others offered to captive birds or snakes. As the mouse approached to attack, the lizard would square around, facing it with open mouth, and sometimes would jump forward at the mouse with a sudden, hissing expiration. Having been brought to bay, the lizard showed no inclination to escape, but usually stood its ground so long as the mouse remained in sight, sometimes even driving it back several inches with a sudden charge. Such fights always ended abruptly with the mouse closing in, at a favorable opportunity, and killing the lizard with a few well-directed bites.

SUMMARY

Populations of fence lizards at Belmont Orchard and Dark Hollow, Jackson County, Oregon, and at Berkeley, Alameda County, California, were studied for five years beginning in June, 1933. The lizards were marked to make them permanently recognizable.

Growth in the fence lizard takes place during three periods. In the first period, between the time of hatching and the time of entering hibernation, growth is rapid but highly variable because of variations in the length of the growth period and in climate. Most of the eggs hatch in August, but some hatch as early as mid-July or as late as mid-September. Newly-hatched young are less than 30 mm. in head and body length and weigh less than 1 gm. They are more terrestrial than adults and more easily captured, and mortality is high among them. They remain active in the fall later than do adults. Most of the growth occurs between the first and second hibernations. When the lizards begin this period, they usually have a head and body length of from 35 to 45 mm. They grow so rapidly that in the fall they often cannot be distinguished from adults. The amount of growth, however, is erratic and unpredictable; individuals of the same age living in the same locality may differ greatly in their growth over a given period; some grow so slowly that they may be mistaken for members of the subsequent year's brood. Following their second hibernation, fence lizards are sexually mature, but their growth continues until fall, after which it ceases, or at least is greatly slowed down.

Adult fence lizards may molt but once a year, in August. In their first growing season the young probably molt several times. In the season following the first hibernation they may molt four or five times.

Extent and rapidity of tail regeneration varies greatly in different individuals; regeneration takes place mainly within a few weeks after the tail is broken.

Males and females pair off during the breeding season in early spring, but pairs are also frequently found in close association at other times of year. Males court females by making characteristic bowing movements, displaying the bright blue of the ventral surface. The same display is used to intimidate other males. Before mating, the female is shy and elusive. Gravid females are aggressive and will not tolerate courting by males. Eggs are deposited in May or June in burrows made by the females.

Adults are tolerant but not solicitous of young; the fighting instinct appears early in young males. Males are especially intolerant of each other in the breeding season. They tend to space themselves at intervals, and each selects as headquarters some favorable location which it defends against other males. But territorial boundaries are not sharply defined and are continually shifting. Where food and shelter are abundant, several males may live in close association; under such circumstances one is dominant. Territorial and mating behavior have much in common; in fights between males mating behavior sometimes appears.

Individuals are extremely localized in their movements and may live their entire life within a radius of a few hundred feet; when moved, they do not find their way back to their home territories. Spheres of activity are gradually shifted over periods of weeks or months in response to environmental changes; males move about more than females, probably because of the territorial pressure exerted upon them by other males.

The average life span is short; at Dark Hollow each year there was more than 80 per cent replacement of the population (but some of the replaced individuals were probably still alive, having moved elsewhere). The potential longevity is more than five years.

Fence lizards are preyed upon by many kinds of snakes, birds, and mammals; the yellow-bellied racer is perhaps one of the most effective natural enemies. Fence lizards usually escape their enemies by running and hiding, but may actually take the offensive in driving away small mammals.

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Transmitted by author March 30, 1938.

SPECIATION IN THE AVIAN GENUS JUNCO

BY

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UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOÖLOGY

EDITORS (BERKELEY): J. F. DANIEL, HAROLD KIRBY, S. F. LIGHT, A. H. MILLER

Volume 44, No. 3, pp. 173–434, 33 figures in text
Submitted by editors June 9, 1938
Issued May 24, 1941
Price, $3.00

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY, CALIFORNIA

CAMBRIDGE UNIVERSITY PRESS
LONDON, ENGLAND

PRINTED IN THE UNITED STATES OF AMERICA

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SPECIATION IN THE AVIAN GENUS JUNCO

BY

ALDEN H. MILLER

(Contribution from the University of California Museum of Vertebrate Zoölogy)

INTRODUCTION

THE PRIME OBJECT of this treatise on the genus *Junco* is not nomenclatural or taxonomic. The purpose has been to make a thorough analysis of races and species as they occur in nature in order to determine the degree of unity of each, and to trace differentiation from individual variants through successive stages of group differentiation to the species. Particular attention has been directed to hybridization and intergradation, to the effects of different kinds of isolation, to recombination of racial stocks, and to the spreading of comparatively large mutations in populations. From such investigations certain assumptions concerning the evolution of natural units may be made, and some knowledge can be gained of the genetics of characters.

Juncos do not lend themselves to experimental breeding on a scale that will permit the procedure followed in the study of geographic variation in mice (*Peromyscus*) by Sumner (1932). The method must be largely observational, with resort to various analytical devices. Among birds, the genus *Junco* is especially rich in instances of natural interbreeding of well-marked forms, and it shows great variety in degree and kind of differentiation. Although experiments may not be set up and controlled, there is reasonable assurance that some of the conditions of natural "experiments" can be discerned at the same time that the results are emerging.

The author feels confident that, in spite of limitations in method, a significant body of information about the finely graded stages in the process of evolution of species has been gained. Full knowledge of such stages reveals part of the natural mechanism whereby progressive change takes place. Furthermore, it shows what actually is taking place and not what might take place through human experimentation. There is something presumptuous about the current expression "experimental evolution." The extremely important and essential experiments that pertain to certain aspects of evolutionary process have significance according to the degree to which they relate directly to known conditions of natural evolution. Perfection in our knowledge of natural situations is far from realization. The convergence of various approaches upon the problems of evolution will lead to success only as the weight of various types of evidence is felt by investigators whose backgrounds are of different kinds. The approach in this work on *Junco*, although bearing the earmarks of taxonomy, has at least attempted freely to utilize genetic concepts and the ecologic background.

The taxonomic and nomenclatural contributions of this paper do not embody radical departures from previous systems of classification. Ridgway (1901) and Dwight (1918) have contributed the best information on the taxonomy of juncos to date. No new forms are named herein, but some are found to be rather differently constituted than is generally conceived. Emphasis throughout has been placed on breeding series, the previous inadequacy of which Dwight admitted curtailed his solution of many problems. The attention given to intergradational areas in the search for principles of speciation has clarified nomenclatural treatment in some measure. The customary criterion of intergradation, either geographic or morphologic, has been emphasized in arbitrarily defining species and subspecies. Thus the point of view coincides with that of current workers in vertebrate taxonomy and with the rassenkreis principle. But the application of such a seemingly simple criterion as intergradation encounters pitfalls in insular groups, as Rensch (1934, pp. 47–51) has especially well pointed out. Also, even when the full story of natural interrelations of forms is known, I have found that intergradation is not a matter of simple presence or absence. Some kinds of intergradation are in reality partly hybridization and merge over into all degrees and kinds of limited and sporadic hybridization which defy simplification. The more there is known about the variety of interrelations of forms, the less easy is the use of any one criterion.

Nomenclatural matters and lists of breeding localities have been segregated in the appendixes (pp. 381–425) in order to relieve the discussions of races and species of material not essential to the biologic problems. These items are vital to the proper understanding of classification in the genus, and the breeding localities provide information essential to workers concerned with local distributional problems. It is regretted that detailed localities for migrant and winter birds cannot be presented. The cost of printing lists so extended as these is prohibitive. Winter ranges and distributions are sufficiently well outlined to reveal all important features of winter dispersal.

SURVEY OF THE GENUS

The genus *Junco* ranges from the arctic tree line in North America south to western Panama and comprises twenty-one forms. The forms are all geographically complementary and constitute what Rensch terms an "artenkreis." Some distinct subgroups occur within the genus that are fully isolated and strongly differentiated from one another. Thus artenkreise of lesser scope within the entire group may be conceived. The following outline serves to introduce the forms of the genus and suggests the relationships which are detailed later:

- Streaked-backed, dark-tailed junco; *Junco vulcani* (1), Costa Rica, Panama
- Plain-backed, partly white-tailed juncos
  - Yellow-eyed juncos
    - *alticola* artenkreis
      - *Junco alticola* (2), Guatemala
      - *Junco fulvescens* (3), Chiapas, Mexico
    - *phaeonotus* artenkreis
      - *Junco bairdi* (4), Cape district, Lower California
      - *phaeonotus* rassenkreis
        - *Junco phaeonotus phaeonotus* (5), southern Mexican highlands
        - *Junco phaeonotus palliatus* (6), northern Mexico, southern Arizona

- Dark-eyed juncos
  - Red-backed juncos
    - *caniceps* rassenkreis
      - *Junco caniceps dorsalis* (7), central Arizona, New Mexico
      - *Junco caniceps caniceps* (8), Nevada, Utah, Colorado
  - *oreganus* artenkreis
    - *oreganus* rassenkreis
      - *Junco oreganus mearnsi* (9), Wyoming, parts of Montana and Idaho
      - *Junco oreganus montanus* (10), interior of British Columbia, Washington, and Oregon
      - *Junco oreganus shufeldti* (11), coastal Washington and Oregon
      - *Junco oreganus oreganus* (12), southern Alaska, central coastal British Columbia
      - *Junco oreganus thurberi* (13), Sierra Nevada and mountains of southern California
      - *Junco oreganus pinosus* (14), central coastal California
      - *Junco oreganus pontilis* (15), Sierra Juárez, Lower California
      - *Junco oreganus townsendi* (16), Sierra San Pedro Mártir, Lower California
    - *Junco insularis* (17), Guadalupe Island, Lower California
  - *hyemalis* artenkreis
    - *Junco aikeni* (18), Black Hills, western South Dakota
    - *hyemalis* rassenkreis
      - *Junco hyemalis cismontanus* (19), interior of northern British Columbia
      - *Junco hyemalis hyemalis* (20), Boreal forests of continent, Alaska to New England
      - *Junco hyemalis carolinensis* (21), Appalachian region

It is the belief of the author that a thorough understanding of the natural history of a group is prerequisite to sound consideration of its evolutionary problems. A large body of information relating to the life requirements of juncos has been gathered from a variety of sources, but it is not yet ready for presentation. Several field seasons have been spent in search of factors in distribution, reproductive rate and cycle, foraging method, migration, molt, territoriality, flock behavior, concealing coloration, and recognition marks. Although little special mention of such items will be found, they naturally have had much weight in attacking the problems of speciation. Especially significant have been observations on tolerance in breeding between members of strongly differentiated forms. In some juncos, fundamental differences in behavior coincide with structural differentiation. Particularly is this true of the yellow-eyed juncos (at least, of *palliatus*), which contrast with dark-eyed forms in manner of terrestrial locomotion, song and notes, general temperament, and method of concealment. Such considerations strengthen one's impression of fundamental distinction.

Juncos vary from strongly migratory types to permanently resident forms. This variation involves differences in physiological adjustment which may have important effects in isolating stocks and thus furthering structural differentiation. Nevertheless, the tendency of migration to break down the geographic segregation of populations is apparent in this genus as in other genera of birds (see Miller, 1931, pp. 121–124) where similar conditions prevail. Even in resident species the habits of moving about and flocking in winter operate to prevent extreme local isolation.

Speaking broadly, juncos are a widely adaptable and tolerant type of sparrow that can survive and breed under a variety of local conditions in Boreal and sub-Boreal areas. Usually they are a dominant constituent in point of numbers of Boreal avifaunas (Linsdale, 1932, pp. 223–224). Although they migrate from regions of extreme winter climate, they are among the hardiest of ground-foraging northern fringillids. Differentiations are entirely of a horizontal type, there being essentially no instances of ecologic or zonal segregation in the same geographic region. They do not display striking examples of protective coloration, and the present adaptive value of many of their racial and specific characters is at least not self-evident.

MATERIALS

Field expeditions.—In 1931 active field work was begun. The plan was to visit breeding areas of the various forms of juncos occurring in the Rocky Mountain area. From May 22 to August 1, eighteen successive collecting stations were established, beginning in southern Arizona (Catalina Mountains) and ranging north through the San Francisco Mountain region, along the Wasatch Mountains of Utah and into eastern Idaho to the Yellowstone Plateau. The stations were from 20 to 100 miles apart, in accordance with the problems of local distribution and intergradation that were encountered. The following forms were studied and the boundaries and interrelations of each in this sector were determined: *palliatus, dorsalis, caniceps,* and *mearnsi.*

In 1932, from June 15 to August 1, a similar plan was pursued in Oregon and Idaho. The fifteen collecting stations were distributed in an east–west line from the range of *shufeldti* in the Cascades of central Oregon through the *montanus* complex to *mearnsi* in central Idaho, and in a north–south line from the British Columbian border to the Snake River, within the range of *montanus.* Also, the relation of *thurberi* and *shufeldti* in the Cascades of southern Oregon was studied.

In 1934, from May 13 to June 13, a trip was made to the Fraser River Valley of interior British Columbia, especially the Bowron Lake region near Barkerville. The northern division of the race *montanus* and occasional hybrids with *J. hyemalis* were met with.

In 1937, during a month in the field in Lake and Deschutes counties, Oregon, much attention was directed to the interrelations of *shufeldti, montanus,* and *thurberi.*

In May and June, 1935, an expedition to the mountains of northwestern Nevada served to clarify the status of juncos in the marginal breeding areas there. In 1936, further time was spent in late May with *Junco phaeonotus palliatus* in the Chiricahua Mountains of Arizona. In California, field work in the coastal area from Humboldt County to San Luis Obispo County has been carried on irregularly, as opportunity offered, in the course of the last six years. All materials obtained on field expeditions are now in the California Museum of Vertebrate Zoölogy.

Total number of specimens examined.—The grand total of specimens used in connection with the work was 11,774. The working collection assembled at the Museum of Vertebrate Zoölogy numbered 4486. However, totals in themselves mean little, and it must be stressed that the examination of many hundreds of winter-taken *hyemalis,* for example, was cursory in the extreme and in keeping with their slight value. The critical material representing birds on their breeding grounds totaled 4552. This number, compared with the 500 breeding birds available to Dwight in 1918, indicates the opportunities which have been presented to me.

Collections studied.—In the summer of 1933 the juncos in the collections listed below were examined:

Colorado College, Colorado Springs (kindness of Mr. E. R. Warren)
Colorado Museum of Natural History, Denver (kindness of Mr. J. D. Figgins)
University of Colorado, Boulder (kindness of Mr. H. G. Rodeck)
University of Kansas, Museum of Birds and Mammals, including the Alexander Wetmore Collection, Lawrence (kindness of Mr. C. D. Bunker and Mr. W. S. Long)
Carnegie Museum, Pittsburgh (kindness of Mr. W. E. C. Todd)
United States National Museum, Washington, D.C. (kindness of Dr. Alexander Wetmore and Dr. Herbert Friedmann)
Biological Survey Collection, U.S. Nat. Mus. (kindness of Dr. H. C. Oberholser)
Philadelphia Academy of Sciences (kindness of Dr. Witmer Stone)
American Museum of Natural History, New York, including the collections of J. Dwight, Jr., L. C. Sanford, and J. T. Zimmer but not the Rothschild Collection (kindness of Dr. Frank M. Chapman and his staff)
Museum of Comparative Zoölogy, Harvard, including the collections of John H. Thayer, C. F. Batchelder, A. C. Bent, and F. H. Kennard (kindness of Mr. J. L. Peters and Mr. Ludlow Griscom)
Field Museum of Natural History, Chicago (kindness of Dr. Wilfred Osgood and Mr. Rudyerd Boulton)

In the summer of 1934 the juncos in the following collections were examined:

National Museum of Canada, Ottawa (kindness of Mr. P. A. Taverner)
Royal Ontario Museum of Zoölogy, Toronto (kindness of Mr. J. H. Fleming)
J. H. Fleming Collection, Toronto
British Museum, London (kindness of Mr. N. B. Kinnear)
Berlin Museum, Berlin (kindness of Professor Dr. Erwin Stresemann)

Certain juncos have been examined in the Leland Stanford Junior University Collection (kindness of Professor Willis H. Rich) and in the Louis B. Bishop Collection at Los Angeles.

Entire collections or important parts of collections have been lent to me for extended examination in connection with the museum material at Berkeley:

Biological Survey, through Dr. Harry C. Oberholser
D. E. Brown
California Academy of Sciences, through Mr. Harry S. Swarth and Mr. James Moffitt
California Institute of Technology (Donald R. Dickey Collection), through Mr. A. J. van Rossem
John Cushing
William B. Davis
Ralph Ellis
Reed Ferris
Laurence M. Huey
Randolph Jenks
Stanley G. Jewett
J. Eugene Law
Los Angeles Museum of History, Science and Art, through Mr. George Willett

J. and J. W. Mailliard
T. T. and E. B. McCabe
D. D. McLean
University of Michigan (including Max Minor Peet Collection), through Dr. Josselyn Van Tyne
Museum of Northern Arizona, through Mr. Lyndon L. Hargrave
Provincial Museum of British Columbia, through Dr. Ian McTaggart Cowan
San Diego Society of Natural History, through Mr. Laurence M. Huey
United States National Museum, through Dr. Herbert Friedmann

Acknowledgments.—To the persons represented in the foregoing lists who have sent specimens or who have courteously made collections available for study I wish to express my very great appreciation. Many have contributed information in letters or in conversation that has been of distinct importance. Without the interest and coöperation of this large group of ornithologists the scope of the work would have been seriously curtailed.

It is a pleasure to acknowledge special assistance received from several sources. Financial support of field work in 1931 and 1932 was provided by grants from the Board of Research of the University of California. Assistance from the Work Projects Administration, Project A.P. 165–03–6079, has been had in the preparation of maps and manuscript. Mr. Lyndon L. Hargrave has, among other courtesies, sent me live juncos from Arizona for purposes of experimental breeding. Mr. Harry S. Swarth gave me the benefit of his wide experience with juncos by contributing criticism and counsel. Dr. Lewis W. Taylor, of the Division of Poultry Husbandry, University of California, coöperated in arranging facilities for captive birds. Mr. T. T. McCabe for a number of seasons directed special attention to the assembling of critical material from British Columbia; his intelligent and energetic pursuit of my problems in the field has been highly valued. Mr. A. J. van Rossem carefully examined and furnished reports on types of juncos in Old World museums. Dr. William B. Davis has obtained some especially significant material for me in Idaho. The continued support of the Museum of Vertebrate Zoölogy through its former director, the late Dr. Joseph Grinnell, was most encouraging, and a variety of facilities was placed at my disposal. The assembling of data from specimens in museums visited in 1933 was possible on the scale attempted because of the assistance of Virginia D. Miller; also in matters of field work and measurements her efforts have been a large factor in the bringing of this work to completion.

METHODS OF ANALYZING CHARACTERS

Pigmentary characters were analyzed in two ways. The total color effect in a given area of plumage was matched with a graded series of samples, selected to represent approximately equal degrees of difference in color. For example, twelve grades of black and gray were recognized, and typical samples were selected for use in designating variants in head color in a number of the northern forms of the genus. It was not feasible to employ a color wheel for standardizing the analyses, because of the variety of places where examinations were conducted. Type samples of variants were always carried with me when determinations were attempted. Much effort was directed toward establishing equivalents of variants in worn and fresh plumage. Careful comparison of stages in wear, consideration of feather structure and pigment distribution, and study of molting birds has made possible a fairly safe identification of colors of the breeding plumage with their initial appearance in fresh plumage. The majority of critical analyses of coloration have been made on breeding birds in spring plumage before the feathers were badly worn. Ideally, all the basic comparisons should be made on fresh-plumaged birds taken while still on their breeding grounds in late summer; but practically this is impossible, since so far as many northern races are concerned the period over which such birds might be collected would be only two weeks.

A second phase of color analysis has been simple microscopic examination of feathers to determine types of pigment present in various parts of the feather. In juncos there appear to be no lipochromes in the plumage, but only melanins. The melanins apparently fall into the two major classes defined by Görnitz (1923, pp. 468–469): eumelanins, dark brown, gray, or black pigments, frequently peripherally distributed in barbules; and phaeomelanins, reddish brown, pink, and yellow. Although Görnitz points out that there is no absolute distinction between these two kinds, in *Junco* the pigments almost always fall obviously into one class or the other.

The types and distribution of pigments differ in important ways. For example, eumelanin may be entirely absent from an area of the plumage in one species, but present in that region in another. Nevertheless, microscopic study has not revealed a sound basis for much of Dwight's (1918) system of quantitative and qualitative color differences. In general, fewer basic qualitative differences are found than he indicated. If eumelanin grades into phaeomelanin by successive degrees of oxidation, as Görnitz's work indicates, is not this a finely graded quantitative change? Even the fundamental distinction in these two classes of melanins is not, in one sense, qualitative.

The annual molt of juncos is the only one of any importance. The prenuptial molt is nearly obsolete and effects no material change in appearance. The postjuvenal, or first fall molt, is incomplete; primaries, secondaries, and greater primary coverts are not replaced, and the tail usually is not molted at this time. Juvenal wing and tail feathers carried through the first year are indistinguishable from those of birds a year or more old. The body plumage of the fall immatures in a number of races is different in average coloration from that of adults. But no absolute differentiation has been revealed—a situation also true of sexual dimorphism.

Because of this situation and the fact that the age of but few measurable birds taken on their breeding grounds has been dependably determined from the skull, no segregation of age groups could be made in the analysis of wing and tail lengths. In one group of fall *thurberi* of known age, the maximum for first-year birds was nearly the same as that for adults. The factor of age composition of samples does not appear to be as important, therefore, as in some other genera, and of necessity is here neglected.

The tail pattern of juncos has been variously regarded in previous work on the genus. No one can reasonably deny that there is a large amount of significant variation. The narrow taxonomic approach minimizes the variations in tail white because great individual variation makes it unusable in practical diagnoses. It appears, however, that tail pattern is relatively stable in an individual. The variation in successive feathers grown from a given feather germ usually is not great, though it is appreciable. This does not prove that the details of pattern are genetically fixed, but only that the feather germ is fairly stable once developed. The variations between right and left sides of the tail of the same bird would not likely be of genetic origin. In analyzing tail variants, only differences larger than those ordinarily encountered between the two sides of the same individual have been considered. Probably they represent in fair measure hereditary differences. Accordingly, each feather was classified separately for the two halves of the vane in respect to whether it was entirely black, black with a white spot, ¾, ½, or ¼ black, white with a black spot, or entirely white. Finer distinctions usually would be meaningless.

Linear measurements from skins, in millimeters, were taken as follows: wing, the chord; tail, from posterior base of oil gland; bill length, from anterior rim of nostril to tip; bill depth at base of culmen; tarsal length; middle toe without claw, from junction with inner toe; hind toe without claw, to base of inner toe (digit II). The greatest instrumental errors are made in the toe measurements. Bill depth was not taken if the mandible was out of place. Juvenal birds were measured for wing, tail, and feet if the flight feathers showed no sheaths. Feather growth has at that time ceased and these same feathers would be carried throughout the first year. The feet attain full growth before the wing feathers. It was found that bill dimensions, especially length, increased through part of the fall in immatures. Bill length is especially subject to alteration from abrasion (see p. 183).

Weights of some series of breeding birds have been available. When seasonably comparable, they may in males be the best practical means of registering the general size of the bird. None of the linear measurements satisfactorily indicate body size, although they reflect differences in size.

VARIATIONS AND INTERRELATIONSHIPS OF RACES AND SPECIES

Treatment of the different forms of juncos may for convenience begin with *Junco caniceps*. It is a central type geographically, and clarification of its relationships lays the ground work for consideration of a number of other species and races. Although related to the brown-eyed northern juncos, in a sense it forms a link with the yellow-eyed juncos. There is no reason to suppose that *J. caniceps* is phylogenetically more important than other rassenkreise.

Rassenkreis Junco caniceps

Gray-headed Junco

The group is composed of two sharply marked races, a southern *dorsalis* and a northern *J. c. caniceps*. They replace each other geographically and interbreed freely in certain isolated areas that are intermediate geographically. The rassenkreis occupies the southern Rocky Mountains and the Great Basin ranges. Migration is irregular, but is definite and fairly extensive in certain members of *J. c. caniceps.*

Principal characters of the group.—Iris dark brown; lower mandible flesh-colored, upper mandible black or flesh-colored. Back with sharply defined mahogany red area, confined normally to interscapular region; red color results from phaeomelanins deposited in barbules, basally in distinct granules, distally uniformly; eumelanins lacking in barbules; tips of feathers grayish because of reduced amount of phaeomelanin pigment. Lores and ocular region black, contrasting with neutral grays of head. Sides gray without line of demarcation separating them from upper breast. Tail always with two, and usually three, outer feathers partly or completely white. Size fairly large, wing of males averaging about 82 mm.

Sexual differentiation in plumage slight. Females average slightly lighter in colors of head and side in race *caniceps* only. Fourth rectrix more often pure black, fifth and sixth rectrices less often pure white in females than in males. Degree of sexual differentiation in rectrices variable, depending on population involved. Size differentiation about 5 per cent in wing and tail, 2 per cent in bill and feet. Females often have traces of buff on tips of feathers of sides, and reddish- or buff-tipped wing coverts. A distinctive immature or retarded plumage not recognizable; occasionally young males have buff-tipped sides, and this feature predominates in young females.

The red of the back alters with the season, becoming brighter and yellower to approach burnt sienna and Sanford's brown. The gray tips are worn off early, but this does not seem to affect the tone of color importantly. Brightening is not pronounced until late April, but in the succeeding six weeks the greatest alteration takes place. Since there are no dark eumelanistic deposits in the ends of the barbules, wearing away of these parts cannot account for the change. Seemingly there is an alteration in the phaeomelanin itself under the action of light. Abrasion of the surfaces of the barbs and barbules does not alone explain adequately the brightening of the color. The grays of the head pale slightly, so that the mass effect in worn plumage is that of lighter hood, except in the extreme state of wear of midsummer, when exposure of the basal downy barbules gives a sooty appearance.

Junco caniceps caniceps

Racial characters.—Features present in all individuals that distinguish them from *J. c. dorsalis* are: (1) darker neutral gray (light neutral gray and neutral gray) of hood, especially that of throat, and (2) flesh-colored upper mandible. Averages for the following measurements are lower: tail length 3 per cent, bill length 3 to 6 per cent, bill depth 3 to 6 per cent, tarsal length 2 to 3 per cent, and middle toe length 2 to 6 per cent. The amount of white in the tail averages less (see p. 207).

Nongeographical variation.—The race *caniceps* is relatively uniform. Especially is this true with regard to dorsal coloration, which in seasonally comparable specimens displays none of the variation found in the backs of *J. hyemalis* and *J. oreganus*. Hood color and white in the fourth and fifth rectrices varies individually, but also regionally, and so will be considered separately. White of the outer rectrix is not geographically variable within the race; 7.2 per cent lack an immaculate white outer web; 1.7 per cent lack a completely white inner web.

Reddish color of variable extent is not uncommon on the pileum. It appears in all populations. In the total of 772 *J. c. caniceps* examined, 48, or 6.21 per cent, have some feathers distinctly red, not merely buff tipped. Definitely delimited white spots on wing coverts occur in 1.29 per cent.

Wing, tail, and tarsal lengths are so nearly the same (average differences no greater than 1 per cent and unreliable statistically) in the Nevada, Utah, Colorado, and New Mexico subregions of the breeding area that all breeding birds may be combined for the statistical treatment of these features. (See table 1.)

TABLE 1

WING, TAIL, AND TARSAL LENGTHS IN JUNCO CANICEPS CANICEPS

Measurement	Sex	No. of specimens	Mean with prob. error	Standard deviation	Coeff. of var.
Wing..............	♂	159	81.96 ± .11	1.97	2.40
	♀	81	76.83 ± .17	1.71	2.22
Tail..............	♂	145	74.37 ± .13	2.44	3.28
	♀	72	70.02 ± .18	1.93	2.75
Tarsus............	♂	157	20 31 ± .03	0.58	2.85
	♀	81	20.01 ± .05	0.67	3.30

Correlation for wing and tail is .71 ± .027.

Geographical variations within the race.—Color of hood, varying between neutral gray and light neutral gray, averages the same in Utah, Colorado, and New Mexico. But in Nevada there is a greater proportion of dark-headed types and a very few individuals that are darker than the extremes in the other three regions. Most of the Nevada specimens are from the Toyabe Mountains, western frontier of the *caniceps* rassenkreis. The Nevada group includes birds from the rest of the eastern part of the state except the northern half of Elko County, and all of Clark County, where hybridization with other juncos occurs. The samples from the Ruby Mountains and Snake Mountains, comprising most of the individuals aside from the Toyabe group, differ in no respect from the latter series.

To determine the degree of differentiation in hood character in Nevada examples, 62 breeding males, 30 from southern and central Utah, and 32 from the Toyabe Mountains, were mixed and then seriated according to color of the ventral aspect of the hood. In the darker third, 3 out of 21 were Utah birds; in the lighter group, 4 out of 21 were Toyabe birds. Forty-four per cent could not be segregated into geographic groups on the basis of hood color. In a group of 30 females from the same localities 43 per cent could not be segregated. One bird from the Toyabe Mountains has a peculiar black nuchal crescent, representing the posterior part of the hood dorsally. The rest of the hood is dark gray of the type encountered in other birds of this region.

At least three individuals from central and eastern Nevada have some color in the sides of *J. oreganus* type. One of these is in all respects *shufeldti.* All were taken in the breeding season. There are some other individuals of similar character, not taken on dates that would completely preclude migration, that might also have remained in central Nevada throughout the summer. The significance of these variants will be discussed later, particularly in connection with the relationships of *caniceps* to adjoining species.

The white of the tail tends to be more extensive in rectrices 4 and 5 in Nevada birds. This is best shown in the inner webs of these feathers. Segregation of more than half of the Nevada population from the other *caniceps* groups would be impossible on this character alone.

TABLE 2

PERCENTAGE OF POPULATION OF J. C. CANICEPS WITH INNER WEBS OF RECTRICES SHOWING BLACK OR WHITE

Sex	Colorado	New Mexico	Utah	Nevada
	Percentage with inner web of rectrix 4 all black			
♂	7	5	3	0
♀	10	17	..	6
	Percentage with inner web of rectrix 5 all white			
♂	53	52	39	90
♀	24	33	20	53

The difference between the Colorado–Nevada and the Utah–New Mexico groups in bill length is five times the probable error of the difference and hence is significant statistically. However, it was noticed in comparing the longer bills of the Utah group with the shorter ones of the Nevada group that the tip of the bill was more attenuated in the former. This extreme terminal part is subject to much variation in captive juncos, owing to wear. Most of the Nevada series was taken in the Toyabe Mountains in May, 1930. In this season the birds were delayed in breeding by late snows. Unlike the Utah group, which was nesting and feeding upon insects, they, of necessity, fed upon seeds on the barren ground. Such a factor might account for stubbier and shorter bills. No known seasonal factors can be adduced to explain the short bills of the Colorado specimens. The Colorado, New Mexico, and Utah series are completely comparable seasonally. Nevertheless, the uncertainty regarding inherent differences in bill length in Nevada throws doubt upon differences among these other groups.

No reservations need be made concerning bill depth. This measure is reasonably free from influences attendant upon wear. Depth is greater in Nevada and New Mexico than in Colorado and Utah. The differences are three to five times the probable errors and are equally manifest in both sexes.

Length of the middle toe is greater in Nevada and New Mexico than in Colorado and Utah. The differences are only two to three times the probable error, but because they occur in both sexes and parallel differences in bill depth they are thought to be significant.

TABLE 3

MEASUREMENTS OF DIFFERENT POPULATIONS OF J. C. CANICEPS

A. MALES

Measurement	Pop.	No. of specimens	Mean with prob. error	Standard deviation	Coeff. of var.
Bill	Colo.	49	8.28 ± .03	0.36	4.34
	N. M.	18	8.56 ...	....	....
	Utah	37	8.57 ± .03	0.29	3.38
	Nev.	50	8.22 ± .04	0.35	4.25
Bill depth	Colo.	38	6.27 ± .03	0.29	4.62
	N. M.	16	6.50 ...	....	....
	Utah	37	6.26 ± .03	0.23	3.67
	Nev.	46	6.43 ± .03	0.30	4.66
Middle toe	Colo.	41	11.52 ± .05	0.45	3.90
	N. M.	21	11.79 ...	....	....
	Utah	37	11.59 ± .05	0.46	3.96
	Nev.	51	11.81 ± .04	0.41	3.47

B. FEMALES (*averages*)

Pop.	No. of specimens	Bill	Bill depth	Middle toe
Colo.	23	8.16	6.12	11.23
N. M.	12	8.33	6.40	11.41
Utah	12	8.24	6.20	.....
Nev.	35	8.22	6.34	11.41

In summary, partial differentiation geographically within the race involves head color, tail white, and bill depth, less certainly bill length and toe length. The color characters as well as the dimensional characters blend from one extreme to the other. Probably each is inherited through some mechanism of multiple factors—a supposition which is further supported by evidence from naturally occurring hybrids with other races. One population contains a greater number of individuals that approach one extreme (homozygous for many allelomorphic pairs?) than do other populations, but all populations contain occasional extreme individuals. The Nevada population has a higher frequency of variants with dark head and extremely white tail. Both the Nevada group and the New Mexico group show greater average bill depth and toe length. Nowhere is the geographical segregation of characters high enough to make practical any nomenclatural innovations. These incipient differentiations are, however, significant stages in racial evolution.

Distribution in breeding season.—The areas here mentioned are those in which *J. c. caniceps* breeds in pure form, that is, in populations showing no decisive evidence of hybridization or geographic intergradation.

The spotted distribution of this junco must be emphasized. It inhabits for the most part a series of mountaintop islands above 7000 feet in the arid Rocky Mountain and Great Basin ranges. Associations in which it breeds include coniferous forest types dominated either by spruce (*Picea*), *Pseudotsuga, Pinus contorta, Pinus ponderosa, Pinus flexilis,* or fir (*Abies*). It also breeds in pure stands of aspen (*Populus tremuloides*) and of mountain mahogany (*Cercocarpus ledifolius*). Compared with *Junco oreganus,* it shows high tolerance for arid forest and ground cover. It may occupy aspen groves where there is no surface water within two to five miles of the nest site. Unshaded forest floor with the ground poor in humus and nearly lacking in green plant cover is unsuitable for breeding.

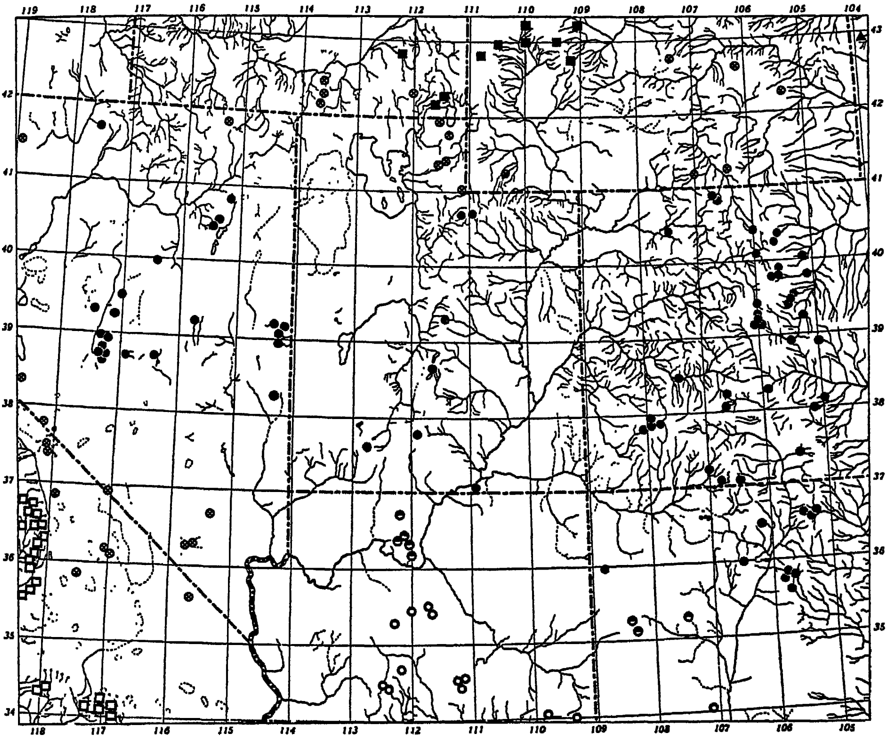

Fig. 1. Distribution of *Junco caniceps caniceps* and neighboring forms in the breeding season. Great Basin and central Rocky Mountain region of United States (Utah, and parts of eastern California and Nevada, southern Idaho and Wyoming, northern Arizona and New Mexico). Each symbol represents a locality from which specimens have been examined. Dots, *J. c. caniceps;* circles, *J. c. dorsalis;* half dots, intermediates between *caniceps* and *dorsalis;* circles enclosing cross, hybrids of *J. c. caniceps* and *J. o. thurberi* (in west), or *J. o. mearnsi* (in north); solid squares, *J. o. mearnsi;* open squares, *J. o. thurberi;* triangle, *J. aikeni.*

Colorado.—Chiefly in Boreal Zone (Cary, 1911) in mountains west of longitude 105°, including the ranges forming the continental divide and such outlying mountains as the Medicine Bow Range, Williams Fork Mountains (Routt County), San Miguel Mountains, Pike's Peak, Sangre de Cristo Range, Culebra Range, and the Wet Mountains; probably also on the Uncompahgre Plateau.

New Mexico.—Chiefly in Boreal Zone (Bailey, 1928, pp. 7, 8, 742, pl. 1) in the Sangre de Cristo, Jemez, San Juan, and Chuska mountains in the northern part of the state.

Arizona.—Mountains of northeastern Apache County, adjoining the Chuska Mountains of New Mexico.

Utah.—Uinta and Wasatch mountains from southern Summit County southward through the mountains of the central part of the state to the Pine Valley, Parowan, and Escalante mountains; in the southeastern section in the Navajo and La Sal mountains (Tanner and Hayward, 1934, p. 232), and presumably also in the Henry and Abajo mountains; probably also in the Deep Creek Mountains on the Nevada border.

Nevada.—Restricted areas in mountains of east-central section of the state: Ruby, Snake (Wheeler Peak), Shell Creek, White Pine, Roberts, Monitor, Toquima, Toyabe, Shoshone and Cedar ranges. Also in Santa Rosa Mountains of Humboldt County, although additional samples from this range might reveal a hybrid population.

Wyoming.—Mountain ranges along the Colorado and Utah borders such as the northern Medicine Bow and Sierra Madre ranges and the Uinta Mountains in the vicinity of Fort Bridger have breeding populations that show traces of intermixture of character with *mearnsi.* Although birds in this area are usually typical *caniceps,* no pure population is known from the state.

Distribution in winter.—Winters abundantly in the mountainous sections of Arizona and New Mexico. Also occurs in Colorado along the east base of the mountains and south through western Texas (Chisos Mountains) and Sonora and Chihuahua to northern Durango. The bird rarely moves eastward any great distance onto the plains. There are records for south-central Nebraska (Red Cloud), Kansas (no. 24040, Acad. Nat. Sci. Phila., W. S. Woods, 1859, no locality), and Oklahoma (sight record, Nice, 1931, Norman, Cleveland County). Probably *caniceps* winters in parts of Nevada, but winter-taken specimens have not come to hand. They occur at least in southern Utah (Presnall, 1935, p. 209). Occasionally winters in coastal southern California (6 specimens), as far south as San Diego County. A report from Michigan (Allen, 1879, p. 123) is not well authenticated. In Arizona the birds usually frequent the foothill districts, especially the oak association.

Relationships with adjacent forms: J. c. dorsalis.—Populations of intermediate and mixed character exist on the Kaibab Plateau in northern Arizona and in the Zuni Mountains in New Mexico. Twenty-one breeding males are available from the Kaibab region. They show that *dorsalis* and *caniceps* interbreed freely. In collecting this series in the summer of 1931, I saw no evidence of segregation of the two types in the field. Each bird reacted to other juncos in the same fashion irrespective of bill and head color.

The Kaibab population affords opportunity for analysis of a kind of intergradation frequently found between geographic races of birds. Seven characters are worth considering in these racial hybrids: color of upper mandible; color of head; length of tail, bill, tarsus, middle toe; and depth of bill. *Dorsalis* is significantly greater than *caniceps* in these measurements and possesses a black upper mandible rather than a flesh-colored one (see fig. 2). The head of *dorsalis,* especially the ventral surface, is lighter than in *caniceps.* Samples of *caniceps* from points in southern Utah nearest (35 miles) the Kaibab Plateau and of *dorsalis* from the plateau south of the Grand Canyon of the

Colorado (50 miles distant) give no suggestion of a gradient in character toward the region of intermediacy. In each adjacent region the characters average the same as for the rest of the race of which the birds are a part; in *caniceps,* the same as for the Utah region. The question arises whether the intermediates are an intermediate stage in differentiation, having evolved *in situ,* or are the result of interbreeding of the two fully differentiated parental types. We may assume that the latter is the true state of affairs, since both parental types are present, and because the characters of these races show no certain correlation with environmental conditions that would suggest origin of intermediates at this spot.

Head color in the Kaibab series was classifiable into five groups. The birds first were seriated and certain faint breaks in the seriation determined. The range of color variation was slightly greater than that in the Utah–Nevada comparison (see p. 182) and of course involved different absolute values. The five classes are: (1) darkest group, equivalent to the average of Utah birds and equal to the darker members of the lighter third of the Utah–Nevada seriation; (2) equivalent to the four lightest birds of the Utah group; (3) intermediate birds, lighter than any *caniceps* and slightly darker than any *dorsalis;* (4) equivalent to *dorsalis,* but darker than average; (5) equivalent to average *dorsalis,* or lighter than average.

Frequency distribution of these types in order was: 3:4:6:4:2. This is remarkably suggestive of phenotypic ratios derived in hybrid generations subsequent to the F_1 where two or three pairs of multiple factors are in operation. The ratio for three pairs reduced to comparable figures is ⅓:2:5:7:5:2:⅓. The extremes appear only once in 64 times and probably would not occur in a sample of 20. The ratio with two pairs of factors would be 1:4:6:4:1. It might be assumed that the terminal members of the ratio in the intergrades are augmented by immigration of a few pure *dorsalis* and *caniceps* types. There is no evidence of simple dominance of either head type. Apparently the two parental stocks have contributed about equally to the population.

Bill color in these same individuals was classified on the basis of field notebook sketches of the color areas made when the birds were in the flesh. These sketches have been checked with the appearance of the bill in the dried skins. Certain alterations may occur in drying, and the original drawings then prove vital to an accurate recording of the bill color. Figure 2 shows successive stages in the pigmentation of the upper mandible. The first three are types that occur normally in *caniceps.* The first, without any black except for the pit of the nostril, is rare. Types 2 and 3 are equally abundant. Types 8 to 10 are characteristic of *dorsalis;* most individuals are solid black. Types 4 to 7 are found, with rare exceptions, only on the Kaibab Plateau and in the Zuni Mountains. Progressive pigmentation takes place by increase in the size of the basal and terminal black areas until they meet on each side, lateral to the culmen. The basal part of the culmen may or may not be pigmented. The Kaibab birds could be classified into the stages as figured, although there was some variation in the manifestation of each type.

The genetic mechanism is not readily apparent from inspection of the frequency of occurrence of these bill types. Types 2 to 9 occurred on the Kaibab Plateau as follows: 2:6:3:2:2:3:3:1. Pigmentation of the basal part of the culmen occurs independently of the general extension of pigment elsewhere. Thus type 6 is like 4, with the culmen dark, and similarly, 9 is comparable to 7. A single independent pair of factors may control pigmentation of this area. Only 3 out of 22 birds possess black culmens; hence black seems to be recessive to flesh color.

Ruling out the culmen, extension of black on the rest of the bill can be best expressed by the merging of type 6 with 4, and of 9 with 7. The frequency distribution from light to dark is then: 2:6:5:2:4:3. Probably several factors are involved to produce such results. The distribution is bimodal, however, and the several classes might be the variable manifestation of two genetic types corresponding to the two modes. The proportion of these two is 13:9. This approaches the 9:7 phenotypic ratio derived in the F_2 with two pairs of complementary factors. Irrespective of the exact mechanism, there is partial dominance of the light-billed *caniceps* type in the same group of individuals that shows no dominance of *caniceps* head color.

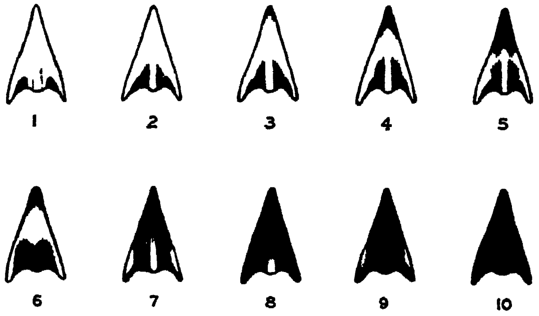

Fig. 2. Dorsal surfaces of bills, showing variation in distribution of pigment. 1–3, *J. c. caniceps;* 8–9, *J. c. dorsalis;* 4–7, intermediates from Kaibab Plateau, Arizona.

Bearing out the evidence for dominance derived from this wild population is the result of a cross of *dorsalis* with *J. o. pinosus* (light-billed), the offspring of which possesses a flesh-colored bill like that of *J. c. caniceps*. The F_1 individual is of type 3 and thus shows the dominance of flesh-colored culmen over black, as also that of the light-billed condition generally.

The average values for the mensurable characters fall about halfway between the values for *caniceps* and *dorsalis,* with the exception of tail length, which is equal to that for *caniceps*. The distribution of size values (fig. 3) shows a small group of three long-tailed birds, equivalent to *dorsalis,* that are separate from the rest of the individuals. This suggests that the long-tailed condition is recessive. There are enough individuals of the dominant, short-tailed *caniceps* type so that in this small sample of intermediates the average happens to be similar to *caniceps,* in fact slightly lower. It should be noted that although wing and tail are correlated in intraracial variations (.71), the differentiation of *dorsalis* from *caniceps* involves a lengthening of tail without correlated lengthening of the wing. It would appear that there are factors governing the ratio of wing and tail and, in addition, factors independent of them which determine a correlated variation in the length of the two.

Bill length shows a distinctly bimodal curve in the Kaibab hybrids, with the greater mode representing the *caniceps* type. This approximates a 9:7 ratio of F_2 hybrids with two pairs of complementary factors, just as in the extension of the dark areas on the bill. Length and color are not correlated in these hybrids and therefore cannot depend on the same factors, nor upon linked factors.

Variations in the other three measurements display normal curves, with averages intermediate between the two races. They conform to the pattern of variation encountered in the inheritance of quantitative characters by multiple factors. No appreciable correlation was found between these characters, nor between any of them and the color of the head.

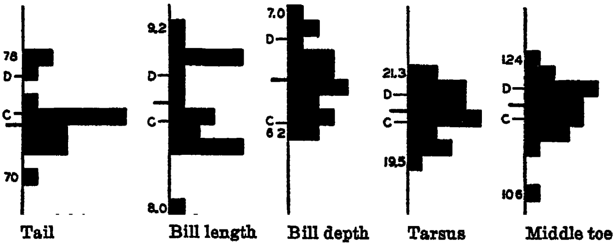

Fig. 3. Individual variations in dimensions (mm.) in intermediates between *J. c. caniceps* and *dorsalis* from the Kaibab Plateau, Arizona. D, average value for *dorsalis;* C, average for *caniceps;* heavy horizontal marker, average for intermediate population.

On the Zuni Mountains of New Mexico three significant specimens have been taken by E. A. Goldman. One of these is in all particulars *caniceps* and another is just as distinctly *dorsalis*. The third is intermediate in head color and of type 6 bill. These three specimens, perhaps supplemented by observations of other birds, seemingly formed the basis for Cooke's statement (Bailey, 1928, p. 743) that *dorsalis* and *caniceps* bred at the same locality and hence were "full species." Doubtless the intermediate bird was referred to *caniceps* because it lacked a completely dark upper mandible. In the light of our knowledge of the Kaibab situation, these three birds give every indication of a similar mixed population on the Zuni Mountains, and they fail to argue for specific distinctness of the two forms.

There are specimens of *dorsalis* at hand from localities near the Zuni Mountains and from the San Mateo Mountains of Valencia County in the same latitude. Larger samples might reveal mixtures at these localities also.

Junco oreganus thurberi.—The interbreeding of *caniceps* with the strikingly different *thurberi* was first suggested by van Rossem (1931, pp. 330–331) in his account of the peculiarly heterogeneous populations of the Charleston and Sheep mountains of southern Nevada. Many of the essential features of these groups were remarked by him. He indicated that head color and side color varied from a *caniceps*-like condition to that of *thurberi* in his series, but that there was no correlation of these characters in individuals. "The most constant character in the series is the red back," which is close to *caniceps* in tone. Van Rossem made two proposals which he thought merited serious consideration in accounting for the variations within these colonies which are out of contact with other populations of breeding juncos. These were that "there may be here a blending of races because of the simultaneous occupation of formerly unoccupied territory by two or more distinct types, or else because of an invasion of the range of an established form by radiations from another area," or that "the unit may be a formerly stable race which is now changing by a series of mutations into another type." In connection with the first proposal, he states that "this population was probably derived either from Junco *caniceps,* or the ancestral stock of which *caniceps* is the present day expression. The dilution of this original stock may have come from *thurberi,* which is resident in the mountains some 150 miles to the west . . . or from *Junco oreganus shufeldti* Coale [= *montanus*] . . . which is the common wintering one in this region. While on geographical grounds *mutabilis* [= the Charleston Mountain population] could conceivably be the result of a fusion of *caniceps* with *thurberi* and while there is evidence of such fusion in the variability of head and side color, the uniformly red backs in both sexes, in which no suggestion of the back color of either *thurberi* or *shufeldti* is apparent, rather militates against this supposition." This latter argument concerning back coloration I do not consider valid. Evidence which I now have of interbreeding of these races in other regions, such as the White Mountains of California, points to the dominance of the *caniceps* back in hybridization. Further, a close study of the backs of van Rossem's Charleston Mountain series reveals that certain of the birds, chiefly those with *thurberi* head, have some mixture of back character. The *caniceps* back does predominate, but seemingly because of genetic dominance.

Van Rossem appears to favor the mutational hypothesis partly because of this supposed lack of blending in the back. He uses mutation in the older sense of the term—as applying exclusively to large or striking alterations. Such a veritable explosion of mutations, locally concentrated as would be necessary to produce the Charleston Mountain group, is so much at variance with conditions now existent elsewhere in the genus and with natural conditions among avian species generally as to be highly improbable. Even in the genetics laboratory such a situation arises only under excessively abnormal treatment such as that imposed by artificial radiation. Mutations, though undoubtedly the basic units out of which species of juncos have been built, are, as usual, infrequent in occurrence in this group.

It is also difficult to explain as a coincidence the fact that all these supposed mutations of the Charleston Mountain group are characters of a kind to be found normally in the adjacent species. None of them is really new or incapable of being produced by various assortments of factors in interbreeding. Other populations similarly diverse in character are found in the genus only in areas between races or species. The mutation argument recalls the classic example of *Oenothera* expounded by De Vries, in which frequent mutations of a striking sort later proved to be in large part the result of an earlier hybridization of species.

Van Rossem's first proposal holds much merit and, in the light of substantiating information on similar populations not available to him, will be adopted as the most tenable view. Contributory evidence will be apparent in the analyses of *caniceps–thurberi* mixtures in the Grapevine, Panamint, Inyo, White, Walker River, and Pine Forest mountains along the western side of the Great Basin.

The characters which differentiate *caniceps* and *thurberi* and which are to be considered in the analysis of interbreeding are color of head, distinctness of hood mark, color of sides, color of back, length of wing, tail, bill, and tarsus, and depth of bill.

The Charleston and Sheep mountains, Nevada.—The nearest known breeding colony of typical *caniceps* is in the Pine Valley Mountains of Utah about 150 miles from the Charleston Range, 100 miles from the Sheep Mountains. The nearest breeding colony of *thurberi,* and this of a somewhat mixed nature, is in the Panamint Mountains, 85 miles distant from the Charleston Mountains. Pure populations of *thurberi* are 150 miles distant, west of Owens Valley. Scattered pairs of birds breed in isolated Transition areas to the south of Charleston Peak on Potosi Mountain, in the same range, and on Clark Mountain, San Bernardino County, California (Miller, 1940, p. 163). Because these birds are similar to those of the Charleston area, they may be considered as part of the Charleston–Sheep Mountains group. With such distances involved, these annectent colonies present a situation somewhat different from that between *caniceps* and *dorsalis* on the Kaibab Plateau. Chance for equal increments from adjacent pure forms would be less, although *caniceps, thurberi, shufeldti,* and *montanus* may all winter in the area or pass through in migration, affording opportunity for hybridization should they by chance remain to breed. The characters of the Charleston group furthermore suggest not a stock to which *thurberi* and *caniceps* contributed equally, but, even discounting dominance, one in which the *caniceps* type is the more prevalent one. More of the *caniceps* type entered into the original implantation, or else, as van Rossem suggests, there was an original *caniceps* stock which has had *thurberi* or *shufeldti* [*montanus*] stock added to it. However, there is the possibility that an originally equal mixture, when isolated, may have had the averages of characters shifted toward one extreme or the other, either through selection or through periodic reduction in numbers with repopulation from small residua.

The Charleston series of 23 summer resident males, plus 2 from the Sheep Mountains and 1 from Clark Mountain have been sorted with respect to head color. The color categories are: (1) average male *caniceps* of Utah; (2) dark male *caniceps* of central Nevada; (3) intermediate tone of gray, equivalent to *mearnsi;* (4) light-headed female *thurberi;* and (5) average female *thurberi.* All male *thurberi* are somewhat darker than this fifth type, so that classes

3–5 are in reality intermediates; no types equivalent to male *thurberi* occurred. Frequency of occurrence of the head types in the southern Nevada series was 6 :7 :6 :2 :4. Several genetic factors would seem to be involved without dominance of one type over the other. The predominance of *caniceps*-like heads is in keeping with the general prevalence of the characters of this race in the sample. The second category is a type of *caniceps* head encountered almost exclusively, but not uniformly, in Nevada.

Females of the Charleston–Sheep Mountains series do not attain head color quite equal to pale female *thurberi*. Individuals fell into three classes: (1) average female *caniceps* of Utah; (2) average female *caniceps* of Nevada; and (3) intermediates near *thurberi*, slightly darker than male *caniceps*. Frequency occurrence was 6 :5 :4. Thus 73 per cent are indistinguishable from *caniceps*, whereas in males only 54 per cent are indistinguishable. The greater sexual dimorphism of the head in *thurberi* may have some bearing on this difference.

The pigments of the sides of *caniceps* and *thurberi* do not blend in the hybrids. The mass effect may appear intermediate or blended, but the pigment granules are either of one type or the other. In *caniceps* the barbules are transparent under the microscope, except distally, where there is blackish eumelanin. In *thurberi*, terminal eumelanin is lacking and faint yellowish phaeomelanin is scattered, sometimes quite regularly in granules throughout the barbule, being quite as prominent basally as distally. In hybrids the areas of a feather that are yellow-pigmented (mass effect pinkish) are usually lacking in eumelanin in the distal parts of the barbules. One half of the vane may be predominantly pinkish, the other gray. The basal part of the vane is pink more often than are the tips. Certain individuals have a wood brown color such as is found in *montanus* and *shufeldti*. In these all the barbules have yellow pigment but also black tips. This condition might be the result of *montanus* intermixture, but it also could be a product of *caniceps* × *thurberi* with retention of both types of pigment throughout each feather. Even then the pigments do not appear blended under the microscope. The brown color is a summation effect of differently colored parts.

The summer resident males were classified as follows with respect to side color: (1) *caniceps* type, eumelanin terminally, including those with faintly buffish tips that are frequently found among *caniceps;* (2) those with a few feathers with areas of phaeomelanin; (3) those with considerable areas of phaeomelanin; (4) those with full extent of phaeomelanin, evenly distributed, as in *thurberi*, including those of *montanus* type as described above. Frequency occurrence of these types is 12 :4 :3 :4. Preponderance of *caniceps* types is evident here as in the hood, and again it appears to be not a case of dominance of one character but of greater proportion of *caniceps* individuals entering into the parentage. It should be noted that some birds attain full *thurberi* character, whereas this was not true of hood color.

The females, classified in the same way, are distributed as follows: 4 :2 :7 :3. Here the distribution favors *thurberi*. This is in agreement with the general trend of sexual dimorphism in the genus, in which phaeomelanins are augmented or unmasked and eumelanins diminished in females. Side-color determiners in these crosses are in some way interactive with sex factors or with sex hormones, just as in the hood. With respect to the sides, this interaction accentuates the *thurberi* character (phaeomelanin), making it really dominant; with respect to the head, it reduces the *thurberi* character (eumelanin).

The foregoing analysis of side color takes little account of the disappearance of eumelanin and the intensity of both pigments. In individuals with hood darker than in *caniceps* and with sides gray, the sides take on the increase in phaeomelanin, in agreement with the hood. This results in a combination of characters resembling to a marked degree certain hybrids between *Junco hyemalis* and *Junco oreganus*. The only distinctly different feature in such birds is the brilliant red back of *caniceps*. This darkening of the sides correlatively with the hood occurs only when the *thurberi* side factors are absent, but then invariably. It suggests an independent factorial control of intensity of eumelanin which may apply to any part of the body plumage carrying such pigment, but which is inoperative for a region when other factors suppress or replace that type of pigment. One set of controls determines whether the side pigmentation shall be eumelanin or phaeomelanin. If eumelanin is determined exclusively, a general factor for intensity of eumelanin may exert an influence.

In the brownish, *montanus*-like sides, the eumelanin is never abundant and does not increase with head intensity. The fact that this type of color occurs in *caniceps–thurberi* hybrids close to the range of *thurberi* substantiates my belief that it is in large measure a result of segregation and interaction of factors in the *caniceps–thurberi* cross. Of the 11 males which have phaeomelanin in the sides 4 have this *montanus* color, and of 12 females 4 are of this type.

The phaeomelanin, when present without eumelanin, is often of a redder type than in *thurberi*, so that it resembles *mearnsi*. This initially suggested to me that *mearnsi* migrants in the spring had remained to breed and had contributed these sides. However, if this were the fact, why should so many individuals bear this character when there were many with heads approaching *thurberi* that could not possibly have been derived from *mearnsi* parentage? Also, why was there none showing the greatly extended area of flank color typical of *mearnsi* which is so frequent in *caniceps–mearnsi* crosses in northern Utah? A better explanation is that the phaeomelanins of the side correspond in some measure with the reddish phaeomelanin of the brilliant *caniceps* back. There might be a factor for increased redness of phaeomelanins, much as there was for eumelanin, that affects all areas of that pigment to some degree. All birds with ruddier sides have pure or partly red backs. Not all red-backed birds that have phaeomelanin in the sides have the *mearnsi*-like hue, so that the case is not completely comparable with intensification in the eumelanins. *Mearnsi* as a race does not fall in with the hypothesis of correlated intensity of phaeomelanin throughout the body, for the back is poor in this pigment, whereas the sides are especially well supplied. But it must be remembered that any such intensification factor is subject to modifications by factors controlling each of the special areas in which the pigment appears. I conceive it as not impossible that the *mearnsi* resemblance of certain hybrids is also a result of segregation and interaction of factors in the *caniceps–thurberi* mixture.

It should be stressed that the margin of difference in hue of normal *thurberi* and *mearnsi* is often very slight and that the importance of this slight difference should not be emphasized out of proportion to the truly great differences involving the presence or absence of phaeomelanin in the sides. Of 10 males which have phaeomelanin in the sides 5 have *mearnsi* hue, and of 12 females 6 are so colored.

The demarcation of the hood ventrally is in large part a product of the pigmentation of head and of sides. Either pronounced *thurberi* pigmentation of the head with gray sides, or *caniceps* head with sides well pigmented with phaeomelanin, will yield a fair line of demarcation. *Thurberi* pigmentation of both regions naturally produces the strongest line. If the phaeomelanin of the sides is slight and mixed, it contributes nothing to the demarcation. In eumelanin intensification on the side the hood mark is nevertheless still visible; hence there may be some factor which affects demarcation alone.

Back color, like side color, involves two pigments. *Caniceps* pigmentation consists of an abundant, ruddy phaeomelanin with no eumelanin. *Thurberi* has a slightly paler, less abundant phaeomelanin, with variable amounts of eumelanin distally on the barbules. The pigments of the two types do not blend, the situation being comparable to that in the flank feathers. Intermediate birds often have the lateral webs of the feathers red, the inner webs tannish brown, much as in *thurberi,* owing to the addition of blackish tips on the barbules of this web. Another form of intermediacy is one with the paler phaeomelanin of *thurberi* present without eumelanin, so giving a yellowish color which may or may not be accompanied on the same feathers with areas of normal *thurberi* color (eumelanin tips). Back pigmentation is not correlated with head or side color.

Birds were classified as follows: (1) *caniceps* back; (2) backs with both red (phaeomelanin) and tan-brown (phaeomelanin plus eumelanin) areas; (3) backs with both pale yellowish and tan-brown areas (an uncommon variant in *thurberi*); (4) backs entirely yellow; and (5) *thurberi* back (somewhat variable in hue). Distribution of types in males and females combined was 26 :11 :1 :1 :0. When this ratio is compared with those for head and side color, the predominance of the *caniceps* character is seen to be distinctly greater. One may assume from this, in spite of unequal contributions from parental races, that there is dominance of the red-backed type. The same inequality of contributions of course precludes exact comparison with standard genetic ratios.

Nevertheless, it has been possible to devise a Mendelian mechanism that might produce these results and those noted in the hybrid population of the Panamint–Walker River series. Independently segregating factors, one pair for presence or absence of eumelanin (AA′), and another pair for red and yellow (Rr), interact to some degree. The AA zygomatic formula produces no eumelanin; A′A′ produces the *thurberi* complement of eumelanin; AA′ produces the partial deposit of eumelanin in mixed pattern. RR and Rr produce red, and rr yellow. RR interacts with AA′ to reduce the eumelanin and produce an unmixed red. Such an assumed interaction is called for in this theoretical mechanism by the high proportion of pure reds relative to mixed reds. The proportion expected in a normal dihybrid is 3 : 6, but with this interaction it is 5 : 4. The actual ratio in the Charleston Mountains is 26 : 11. Since in other characters the pure *caniceps* types are twice the expectation in a case of equal *caniceps* and *thurberi* parentage, the 26 : 11 ratio is roughly equivalent to the 5 : 4 with the first member doubled (= 10 : 4 or 27½ : 11). *Caniceps* back would accordingly be determined by the genetic formulae AARR, AARr, or AA′RR; mixed eumelanin and red, AA′Rr; mixed eumelanin and yellow, AA′rr; pure yellow, AArr; and *thurberi* A′A′RR, A′A′Rr, and A′A′rr. *Thurberi* usually would be A′A′rr (rarely AA′rr), but a red phaeomelanin masked by a full complement of eumelanin would in all probability pass as a *thurberi* back even though it should be of a slightly ruddier hue. Absence of *thurberi* types from the Charleston Mountains may be attributed to the small proportion of pure *thurberi* entering into the cross. A mating of AARR with AA′Rr would, in successive interbred generations, produce chiefly *caniceps* back and mixed red with the occasional appearance of yellows, mixed yellows, and *thurberi* about in the proportion (except for *thurberi*) in which they are actually found on the Charleston Mountains. A true *thurberi* back should appear in larger samples.

A single experimental hybrid of *dorsalis* × *pinosus* (see p. 372) involves back characters comparable, if not identical, with *caniceps* × *thurberi*. This F_1 individual is red rather than yellow and thus appears to confirm the dominance of red, for its makeup should be Rr. The eumelanin is not mixed, but is largely suppressed. This may be the result of AA′ in the *pinosus* parent or of a different gene for eumelanin of the back in *pinosus* where this pigment normally is less in amount than in *thurberi*.

Size characters, with the exception of bill depth, have average values lying between *caniceps* and *thurberi*. In all these but the wing the average is somewhat closer to *caniceps*, corresponding to the situation in those color characters in which there is no dominance. Distribution of individuals with respect to size categories presents no departures from a simple curve, except for bill depth. In the *caniceps–thurberi* hybrids the distribution suggests a segregation of the parental values of *caniceps* and *thurberi* (note positions of averages in fig. 4). The coefficient of variability here is accordingly high—5.83 compared with 3.67 to 4.62 in *caniceps* populations. This is remindful of the mode of inheritance of tail length in the *caniceps–dorsalis* crosses. In bill depth in *caniceps–thurberi* hybrids a single pair of factors with *caniceps* dominant is suggested; the ratio is 15 : 4. In *caniceps–dorsalis* crosses, the bill depth presented a simple curve, not a bimodal curve as here, but the difference in the parent stocks was much less. It is not unreasonable to suppose that multiple factors may regulate small size differences within the two major types and between rather similar races, but that there may be a different factorial arrangement, in this instance a single pair, which determines the rather distinct bill types of *caniceps* and *thurberi.*

Other size characters have coefficients of variability no greater than the parent populations, so that, unlike the situation with respect to color characters, there is no evidence of segregation. This situation was met by Sumner (1932, p. 48) in his analysis of inheritance of linear measurements in interracial crosses in *Peromyscus.* The increase in variability in F_2 may not be apparent if many factors are involved (Babcock and Clausen, 1918, p. 185), unless the sample is very large.

None of the dimensions in the Charleston group correlates with color characters—a circumstance which points to complete intermixture of the birds and to completely independent segregation of characters. Wing and tail correlation is .750 ± .060, which is about the same as within *caniceps* (.71 ± .027). Wing and bill, bill and tarsus, and wing and tarsus are in no way correlated. However, bill length and depth are correlated at .61 ± .098, whereas they are not within *caniceps.* Sumner (1929, p. 488) has reported similar phenomena in which characters are correlated in interracial crosses but not intraracially. Sumner concludes that the intraracial variation is to a less degree genetic than that in interracial hybrids. This has already been suggested in regard to bill length of juncos by the variable state of wear of the tip, yet there must be some inherited intraracial variation in the bill apart from wear. It might be that such a difference in the matter of correlation, intraracially and interracially, is due to different sets of factors determining dimensions in each case, one group of factors being linked or common factors, the other not.

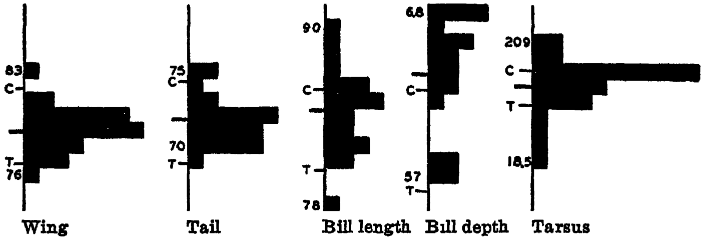

Fig. 4. Individual variation in dimensions (mm.) in hybrids of *J. c. caniceps* and *J. o. thurberi* from the Charleston and Sheep mountains, Nevada. C, average value for *J. c. caniceps;* T, average for *thurberi* of the Sierra Nevada; heavy horizontal marker, average for hybrid population.

Panamint, Inyo, White, and Walker River mountains.—These four mountain ranges lie in a northwest-southeast line, 20 to 50 miles distant from the nearest junco-inhabited territories of the Sierra Nevada. Each is to some degree isolated from the others in the series, so far as junco habitat is concerned. The similar degree of separation from territory occupied by *thurberi* probably accounts for similarity in the amount of departure from the characters of that race. In these mountains, much more so than in the Charleston Mountain population, the characters of the birds are mostly those of one race, *thurberi,* with no typical *caniceps* types occurring. But many characters are in evidence, which are the same as those of the Charleston hybrids. The birds appear not as though *caniceps* had entered into their immediate parentage, but as though some birds of mixed blood from a mountain range such as the Charlestons had crossed with pure *thurberi.* Another possibility is that continual influx from the Sierra Nevadan area has in large part swamped the *caniceps* characteristics.

A classification of characters is employed here which is similar to that used with the Charleston group. Head color for males is never any paler than type 5 (average female *thurberi*). To this series of head categories still darker classifications, type 6 (dark female, extraordinarily light male *thurberi*) and type 7 (average male *thurberi*) are added. Occurrence of head color of males with respect to these three categories was (5) 3: (6) 7: (7) 3. Although the 6th type is not unknown in males of *thurberi,* it would usually occur in about the ratio of 1:10 of the darker type, instead of 7:3.

The females are of head categories 4 to 6 in the following proportions: (4) 5: (5) 4: (6) 2. Class 4 is exceedingly rare in *thurberi.* There is a high proportion of intermediate head types in these samples. It might be suggested that some but not all of the several factors governing head color are heterozygous in these populations.

Of the four side-color types only the first (pure gray eumelanin with intensity increased in correlation with the hood) and the fourth (normal *thurberi*) occur. There are but two of the former. It is curious that there is none with mixed areas of eumelanin and phaeomelanin, but possibly the sample (19 males and females) is too small to include them. The tone of the phaeomelanin pigment is usually normal for *thurberi,* but two approach *montanus* (see p. 192) and two resemble *mearnsi.*

Back color shows decisively the *caniceps* mixture. No pure reds occur, but mixed yellows, yellows, and one mixed red appear. Original parentage of AArr or AA′rr with A′A′rr (*thurberi*) would yield these phenotypes, except for the single mixed red, according to the mode of inheritance previously hypothesized. *Thurberi*-type, mixed yellows (rare in *thurberi*), and pure yellows occur as follows: 10:10:3.

The potentialities in this situation for a new race (or species) are extremely suggestive. If by chance the AArr (yellow) had populated any one of these mountains exclusively and had been sufficiently isolated from influx of other kinds, a uniform race of yellow-backed, blackish-headed juncos of hybrid origin would have appeared. Such a race would be quite comparable to *Junco dorsalis, Junco hyemalis cismontanus,* or *Junco o. pontilis.* This mode of origin is, by itself, no argument against considering such groups as races. The hybrid must be stable and must occupy a definite area to the exclusion of other types if a race is to be established. Such has not been the case on the Charleston Mountains or on the ranges under consideration.

The size characters of the Panamint–Walker River group cannot be fully analyzed, because of the small sample of each sex. All these characters, except bill length, average greater than in *thurberi,* that is, toward *caniceps;* no character attains the average value found in the Charleston series. The averages for these quantitative characters substantiate the view that *thurberi* parentage predominates in this group.

	Wing	Tail	Bill length	Bill depth	Tarsus
Average *thurberi*, ♂.........	76 54	68 65	7.99	5 58	19.62
Average Panamint–Walker River series, ♂............	78.47	70.12	7.76	5 75	19.73

Grapevine Mountains, Nye County, Nevada.—Subsequent to the study of the Panamint–Walker River group a hybrid population was discovered in the Grapevine Mountains on the California-Nevada line east of Death Valley. The series of 21 adults obtained there resembles most the Panamint–Walker River material but contains at least one member that is typical *caniceps*. The group is thus decidedly heterogeneous, possessing extreme parental types of both *caniceps* and *thurberi* and serving to link and further explain the hybrid complexes in the Charleston and Panamint–Walker River series.

Most critical in the series are three birds that show preponderance of *caniceps* characters. None of these has any pink in the sides. One male is typical *caniceps* in all characters and is type 1 head. Another male shows mixed red back and type 4 head, approaching 3. Neither male was taken with a mate. The female *caniceps*-like bird is typical except that the back is mixed red. She was mated to a male with black, type 6 head (light male *thurberi*), typical *thurberi* sides, and mixed yellow back. The general aspect of the pair was that of opposite extremes and if juncos take account of such matters they must have appeared to each other as foreign species.

The pair had two short-tailed juveniles which give some suggestion of segregation of character. The back color of one is definitely red as in young *caniceps*, that of the other more yellow. The genotype of the adults, judging from their external appearance, should have been ♂ rr and ♀ Rr. The segregation in the juveniles is exactly the result expected from such parents. One of the juveniles is more suffused with yellow on the underparts than is the other. This may presage the yellowish side color of adult *thurberi*.

The series of adults, all members included, shows the following phenotypic ratios: Heads of males, (1) 1: (4) 1: (5) 5: (6) 5: (7) 3; females (1) 1: (4) 1: (5) 4. Sides, (1) 3: (3) 1: (4) 17, of which 4 are of *mearnsi* hue, 4 *montanus* hue. Back, red 2: mixed red 2: yellow 1: mixed yellow 4: *thurberi*, 12. Each of the ratios shows more diversity of type than in the Panamint–Walker River series. Fundamentally the population may be said to consist of a group with the same array of genes as in the Panamint–Walker River series but with the addition of a few distinctly *caniceps*-like individuals. The presence of these probably represent recent invasions from the east, either on the part of these birds themselves or their immediate parents. A new injection of *caniceps* blood is currently in evidence, which increment has not yet been thoroughly mixed through the population. Irrespective of the frequency of such an event, there is demonstrated by this infiltration the way in which mixtures of species types undoubtedly have been set up in mountains along the western edge of the Great Basin. The main barrier to this infiltration, which has probably been bilateral, is the series of low desert basins that run more or less continuously from the Amargosa desert northwestward toward the Carson sink.

The Pine Forest Mountains, Humboldt County, Nevada.—This range of mountains provides a limited area suitable for juncos. Three meadows and the adjoining pine-covered slopes, comprising an area of not more than a square mile, appear to be suitable junco habitat. The range is isolated from the Warner Mountains of California, where *thurberi* breeds, by 85 miles of desert. The Santa Rosa Mountains, 50 miles eastward, constitute the nearest station where breeding *caniceps* has been taken; only a single male, active sexually, was procured in the course of three days' special search there. A true population of *caniceps* is not known to exist closer than 150 miles southeast in the Toyabe Range.

Evidence for interbreeding of *caniceps* and *thurberi* on the Pine Forest Mountains is found in a pair that was taken June 5, 1934. These birds were foraging together, the male singing. The female had yellow ova 2 to 3 mm. in diameter. The male was a hybrid *caniceps* × *mearnsi,* with the side color of *mearnsi* and the back of *caniceps.* The female had a dull type of *thurberi* back (which is not, I think, evidence of *montanus* influence), typical *thurberi* sides, and the palest type of female *thurberi* head. On the same date a female *shufeldti* equivalent to the breeding birds in western Washington or northwestern Oregon was taken; it was in breeding condition. Whether this individual would have bred on these mountains is problematical, but it was not a cripple and was behaving like the other female taken on this day. It was foraging in a meadow partly covered with snow, a suitable breeding locality.

The juvenal *thurberi* reported by Taylor (1912, p. 395) from this same locality in 1909 I believe to have been raised on the mountain (Miller, 1935, p. 468). Identification of juvenal individuals is dubious, but certainly the bird is more like young *thurberi* than *caniceps,* although not in all respects typical of the former.

The Pine Forest Mountains occupy a position between the breeding ranges of *thurberi, caniceps, mearnsi,* and *montanus. Shufeldti* may pass through in migration. Very probably the breeding population of the mountains is subject to much seasonal fluctuation and occasional extermination. Stragglers from adjoining races or from zones of hybridization may repopulate it or mix with the resident population. The situation is a duplication in miniature of what took place in the history of the Charleston and Grapevine Mountain groups. Under present biotic conditions there cannot be built up so large a self-perpetuating group of hybrids as in these southern areas.

The facts ascertained relative to the *caniceps–thurberi* contact, and the presence of *shufeldti* in the breeding season on the Pine Forest Mountains and on the Toyabe Mountains (in the latter, not breeding) as stragglers, afford some support for the view that the slight difference in the Nevada population of *caniceps,* consisting chiefly of a larger proportion of individuals with darker type of head, is the result of occasional mixtures with the black-headed juncos to the north and west. Endemic races of other birds in the Great Basin become even lighter colored than Rocky Mountain forms. Why should the juncos be slightly darker headed? Where a multiple factor mechanism is involved, a very small admixture of black-headed birds would be diluted in the fairly large population to produce a number of slightly dark-headed individuals. Dying out of some of the initial hybrids from such a mixture might eliminate certain of the factors for blackness so that heterozygosity in only one pair of the set of multiple factors would prevail. Only one or two phenotypes, closest to the gray extreme, would then appear.

Junco oreganus mearnsi. Northern Wasatch Mountains.—The section of the Wasatch Mountains north of the Uinta Mountains in Utah has a breeding population of hybrids, the proportion of *mearnsi* characters increasing northward until nearly pure populations exist near the Idaho line. Only typical *mearnsi* are known from north of the line in these mountains. Parts of the Wasatch Range have restricted junco habitat and there are occasional gaps in distribution of from 2 to 5 miles.

The first of several localities visited in this section of Utah in 1931 was Kamas (10 miles east), Summit County, at the western end of the Uinta Range. Junco habitat in lodgepole pine and aspen forest was extensive here. Juncos were numerous and all were of pure *caniceps* type. This group may be taken as a starting point in considering the hybrids immediately to the north.

The next locality was Porcupine Ridge, Summit County, 20 miles in an air line north of Kamas and within 3 miles of the southwestern corner of Wyoming. The mountains are low here, consisting of outlying ranges of the Uintas. They are the highest mountains of the uplift extending north to the northern division of the Wasatch. Junco habitat is scarce, with aspens constituting the only cover. Occasional pairs breed in the denser part of this timber. *Mearnsi* characters begin to appear at this point.

A locality 14 miles southwest of Woodruff, Rich County, which was visited, is 30 miles north of Porcupine Ridge. Here there was a moderate amount of aspen timber and a few patches of Douglas fir near the summit of the Wasatch divide. Juncos were somewhat more numerous than at Porcupine Ridge and their habitat more extensive. Between Porcupine Ridge and this region are the relatively low Echo and Weber River canyons, forming an east–west pass. This pass constitutes the most distinct break in breeding habitat along these mountains. From the highway it was observed that in Echo Canyon suitable aspen groves were almost lacking on the mountainsides up to distances of 3 to 5 miles north and south. The junco population in this sector must be very sparse, even more so than at Porcupine Ridge. The Woodruff juncos were exceedingly mixed in character, the proportions of *mearnsi* and *caniceps* types being about equal.

Twenty miles farther north at a point 8 miles west of Randolph, Rich County, another population was sampled in the eastern foothills of the Wasatch Range. Junco habitat is continuous to the south toward the Woodruff locality. Juncos were abundant in the aspen and lodgepole pine forests. The general character of the population was more like *mearnsi* than at Woodruff.

The divide 12 miles west of Garden City, Cache County, was the last locality visited. It is 20 miles northwest of the Randolph region. Abundant aspen, lodgepole pine, and Douglas fir habitat was found here along the crest of the mountains. Habitat appears to be continuous from here southward. The proportion of characters here was the same as at Randolph, with no fewer *caniceps* characters appearing.

Collections from these four stations—Porcupine Ridge, Woodruff, Randolph, and Garden City—show well the shift in frequency of occurrence of characters from *caniceps* to *mearnsi* along this narrow belt of connectant breeding range. But, because there is clearly a varying proportion of the two parental types entering into the mixture at these stations, the genetic situation is difficult to interpret. No one sample is large enough to give reliable proportions of phenotypes. The Randolph and Garden City groups are so nearly alike in proportion that they may be combined, and the Woodruff group might justifiably be added; but the Porcupine Ridge population is evidently so different in parentage that it confuses ratios of occurrence of the separate characters to combine it with the others.

Characters which distinguish *mearnsi* are: blacker head, complete replacement of the gray sides by broad areas of pinkish cinnamon, and dull brown instead of mahogany red back. Size characters and white markings in the tail differ but slightly. The three color characters are not correlated in the hybrids, and any combination of parental and hybrid characters may appear in individuals.

Head color was classified as (1) average Utah *caniceps,* (2) darker Nevada *caniceps,* not entirely absent in Utah but rarely found in *mearnsi,* and (3) typical *mearnsi.* Females were classed in three equivalent categories. Separation of the birds into these categories was difficult because some of them showed extreme wear. The ratio in the Woodruff–Garden City group was 7:10:15. There is evidently a blend of character as in the *dorsalis–caniceps* and *caniceps–thurberi* crosses, the *mearnsi* stage of pigmentation equaling one of the *thurberi–caniceps* intermediate types. Undoubtedly, there are fewer multiple factors than in the *caniceps–thurberi* cross. The proportion of types probably should be about 4:6:4 in an equal mixture of *mearnsi* and *caniceps.* The excess of *mearnsi* in the 7:10:15 ratio may be taken as an index of predominance of *mearnsi* parentage; or about 2 *mearnsi* to 1 *caniceps.* This sample is as predominantly *mearnsi* as the Charleston sample was *caniceps.*

Back color behaves in a manner analogous to that in the *caniceps–thurberi* cross, yet with some significant modifications. Just as in *thurberi,* the *mearnsi* color results partly from eumelanin in the tips of the barbules, which is absent in *caniceps.* The extent of the eumelanin is about twice that in *thurberi,* the mass effect being a much darker, more neutral brown. The phaeomelanin of *mearnsi* is of a pale yellowish character and is not abundant. A factor for *mearnsi* eumelanin may be assumed to be paired with the *caniceps* factor A for absence of eumelanin, much as was the *thurberi* factor. We may call it A^2. As before, AA gives absence of eumelanin; AA^2, mixed areas on the feather; and A^2A^2, uniform eumelanin tips of *mearnsi* type.

The factor governing the yellow pigment of *mearnsi* gives evidence of being dominant to the red, instead of recessive like the factor governing the yellow of *thurberi*. It may be designated R′. The evidence for dominance is found in the prevalence of mixed yellows and yellows over mixed reds and reds in the phenotypic ratios of the Woodruff–Garden City series, and also, significantly, in the appearance of 2 pure yellow to 4 pure red in the Porcupine Ridge group, which in other respects is almost exclusively *caniceps*. A single pure *mearnsi* back also occurs in this latter group. Dominant yellow may alter some AA^2 individuals that otherwise would have had mixed eumelanin to produce uniform eumelanin, just as it was thought the dominant red caused AA to show no melanin in *caniceps* × *thurberi*. The ratio of 20 *mearnsi* to 10 of the mixed type is twice as many *mearnsi* as would be expected, even with the known predominance of *mearnsi* parentage. But such a ratio is expected if an interaction of R′R′ with the AA^2 takes place to complete the eumelanin deposit.

Although the pigments of the back of *mearnsi* resemble those of *thurberi*, their different relative quantities bespeak different factors controlling them. It is not surprising, then, that the dominance with respect to red and yellow and the interaction of factors for eumelanin and phaeomelanin is different where *mearnsi* pigments are involved.

In accordance with the foregoing hypothetical mechanism, *mearnsi* back (1) results from genotypes $A^2A^2R'R'$, $A^2A^2R'R$, $AA^2R'R'$ or A^2A^2RR (ruddy brown, of which few occur); (2) yellow with mixed areas of eumelanin, $AA^2R'R$; (3) red with mixed areas of eumelanin AA^2RR (the difference between this latter and the pure red A A′RR of *caniceps* × *thurberi* lies in the new factor A^2, which produces more eumelanin than A′); (4) pure yellow AAR′R and AAR′R′; (5) pure red AARR. The ratio in the F_2 generation would be 6:4:2:3:1. The ratio in this population with probable 2:1 predominance of *mearnsi* parentage was 20:7:3:2:0.

Mearnsi side color, like back color, appears to be dominant over the gray of *caniceps*. Eumelanin is entirely lacking in the pinkish cinnamon of *mearnsi*, and the latter extends medially onto the breast farther than does the gray of *caniceps;* it may even meet medially along the margin of the hood. The sides of hybrids tend to be either of one type or the other, and in the entire Wasatch group there is only one individual with partly gray and partly pinkish feathers. This is quite different from the *caniceps–thurberi* cross in which mixed feather types were common. Among winter-taken hybrids of *caniceps* and *mearnsi* and in a group of hybrids from northern Nevada several mixed types occur. Perhaps there is some variability in dominance, so that heterozygotes at times are mixed, at other times possessed of the dominant character. If there was no dominance, it hardly seems possible that only one mixed bird would appear in the Woodruff–Garden City series in which other characters show evidence of *mearnsi* blood and in which 4 pure gray *caniceps* occur. The ratio of pinks, mixtures, and grays is 27:1:4. A 27:4 ratio of pinks and grays is to be expected in a cross with a single pair of characters with dominance where *mearnsi* parentage outweighs *caniceps* 2:1. Phaeomelanin and eumelanin are never combined in the same barbule to produce a wood brown color such as is found in certain *thurberi–caniceps* hybrids.

The northern section of the Wasatch Mountains may be conceived of as a narrow connecting bridge, 90 miles long, between the breeding ranges of *caniceps* and *mearnsi*. On the north slopes of the Uinta Mountains *mearnsi* influence appears. North of the most sparsely populated part of the bridge at Echo Canyon a population of mixed origin is found, with *mearnsi* predominating 2:1. The prevalence of *mearnsi* appears even greater because of genetic dominance of certain *mearnsi* characters. In the Salt River Range in Wyoming, pure *mearnsi* occurs. Every year *mearnsi* mingles with *caniceps* in winter and migrates north along this bridge. Which, if either, was the original occupant of the area cannot be determined, nor can it be said whether one or the other is gaining ground now. Hybrids comparable to those found at Porcupine Ridge were taken seventy-seven years ago at Fort Bridger, which is situated similarly at the north base of the Uinta Mountains but is 40 miles east of Porcupine Ridge and not adjoining a breeding area extending northward like that of the Wasatch Range. In terms of years this *mearnsi–caniceps* contact has been of considerable duration without any obvious alterations in distribution of the pure parental races. If migration often carried *caniceps* too far north, or *mearnsi* not far enough north, much more intermixture should result. That such abnormal migration does occur rarely is evidenced by one breeding bird with *mearnsi* sides taken in the range of *caniceps* in eastern Nevada, and by a fully characterized *caniceps* taken in May at Glendive, Montana.

The complete mutual tolerance of the two kinds of birds is shown by the following mated pairs taken in the zone of hybridization: Porcupine Ridge, ♂ pure red back × ♀ pure brown back with young not determinable with respect to back color, and ♂ pure yellow back × ♀ pure red; Garden City, ♂ mixed red × ♀ brown. A pair of birds about my camp west of Garden City was feeding young on July 22. The male was collected at 5 A.M.; it was pure *mearnsi* on back and sides, but with head intermediate. The female, which could be seen to have normal *mearnsi* color on the sides and back, was left with the young. At 10 A.M. the small young were in the same group of bushes with the female, and a new male was on hand, singing, following her with tail fanned, and twittering in characteristic mating behavior; she did not drive him away. This bird was taken and found to have a mixed yellow back, *mearnsi* sides and intermediate head. Female X, as she now became known, had another male attached to her party shortly after 11 A.M. This male was *mearnsi* in all characteristics except for intermediate tone of head. A fourth male came to female X at noon and proved to have pure *mearnsi* back, pure *caniceps* sides, and intermediate head. I am doubtful that these males were all unattached previous to their interest in female X. Males of various sparrows are known to be polygamous on occasion. There was no doubt of the attraction of the female for all of them, however. Not knowing the history of the case, an observer would have considered each to have been her normal mate. No intolerance was evidenced by the female. Some of the males gathered food for the young. This indicates disregard on the part of the junco for differences in colors of sides and backs.

The following list shows the intermixture of back and side types in hybrids, and the predominance of one type or another along the Wasatch Mountains.

Porcupine Ridge
- 4 red back, gray sides
- 2 yellow back, gray sides
- 1 *mearnsi* back, gray sides

Woodruff
- 1 mixed red back, mixed sides
- 1 mixed red back, gray sides
- 1 mixed yellow back, pink sides
- 3 *mearnsi* back, pink sides

Randolph
- 2 yellow back, pink sides
- 1 mixed red back, pink sides
- 2 mixed yellow, pink sides
- 7 *mearnsi* back, pink sides
- 1 *mearnsi* back, gray sides

Garden City
- 4 mixed yellow, pink sides
- 7 *mearnsi* back, pink sides
- 1 *mearnsi* back, gray sides

Southern Wyoming.—Evidence of intermixture is found in a few birds with some mixed areas in the back or with pure *mearnsi* back from the vicinity of Fort Bridger, and from the northern Medicine Bow Range and the Sierra Madre. Other pure *caniceps* from these localities show that the mixture is probably comparable in degree to that in the Porcupine Ridge group.

The Laramie Range and other ranges in south-central Wyoming provide some disconnected junco habitat that forms an incomplete bridge north toward *mearnsi* breeding territory in the Wind River and Big Horn mountains. Evidence of intermixture is at hand from the following mountains in that area (for detailed localities see Appendix and map, fig. 9): Laramie Peak, Rattlesnake Mountains, Casper Mountains.

Northern Nevada and southern Idaho.—There are several mountain ranges north of the Humboldt River drainage of Nevada and the Great Salt Lake desert and south of the Snake River of Idaho in which intermixture occurs. A breeding hybrid bird has been taken just west of the Bear River at Swan Lake, Idaho.

In the Goose Creek and Raft River mountains of Idaho, both pure *caniceps* and hybrids occur. Of 9 breeding birds, 6 are typically *caniceps,* 1 has pink sides, light *caniceps* head, and red back; 1 mixed sides, dark head and red back; and 1 gray sides, light head, and mixed red back.

There is a single breeding hybrid from the Jarbidge Mountains of northern Nevada. Eighteen early September birds taken in these mountains were certainly not far from their breeding grounds. Of these, five have some evidence of *mearnsi* back, six have partly, or entirely, *mearnsi* sides, and only three approach the minimum of light-headed *mearnsi* variants. There are many pure *caniceps.* This suggests that the breeding population of these mountains is principally *caniceps.* A single hybrid is known from the Pine Forest Mountains. Nowhere south of the Snake River, in this sector, are there pure populations of *mearnsi. Caniceps* probably was the original occupant of this area, which *mearnsi* has to some degree invaded. Since *mearnsi* characters are dominant, it is less likely that the reverse has been true.

Summary.—The race *caniceps* is a relatively uniform aggregation of individuals. As in other races, certain peculiar characters unrelated to hybridism or intergradation occur occasionally. These are not correlated geographically. The only geographic variation is found in the Nevada area. This slight difference in Nevada may be ascribed to occasional hybridization in the past with *thurberi,* perhaps also currently. Evidence is at hand of occasional *caniceps* individuals outside of their normal range in the breeding season and of members of adjacent races occurring within the range of *caniceps. Caniceps* will cross with any of the adjacent forms if opportunity is presented. Its geographic isolation from these forms is incomplete in the fact that restricted intervening areas are occupied by mixed populations.

The differences between *caniceps* and *dorsalis* are all either differences in average dimensions or in intensity and extent of the same type of pigment. Regardless of the mode of origin of *dorsalis* or possible complete separation of the race at one time, this race and *caniceps* now behave as do most races at points of interbreeding. Accordingly, they have been grouped in one rassenkreis.

The meeting of *caniceps* with *mearnsi* and *thurberi* results in no less interbreeding than with *dorsalis.* Because of partial isolation, interbreeding cannot take place over large areas, and mixed populations usually are predominantly of one type or the other, owing to proximity to the breeding range of one or the other kind. The characters differentiating these forms involve totally different pigments in certain areas of the body. Although I disclaim degree of difference or qualitative characters as wholly adequate criteria for species, I think they have some weight in these instances. The differentiation of *caniceps* from *mearnsi* and *thurberi* I am compelled to feel is a matter of long standing, and I believe that at times they probably have been completely isolated from one another. It is not easy to visualize their present degree of differentiation as evolving while they have been in continual or even occasional contact. The actual relations of these forms have been fully detailed. The subspecies-species distinction is arbitrary. I believe it will be more useful to consider *caniceps* a separate species from *Junco oreganus* (*mearnsi* and *thurberi*). They are in many ways comparable to the "species" of flicker, *Colaptes cafer* and *C. auratus,* which, however, hybridize over much more extensive areas. At the same time it is most useful to designate the *caniceps–dorsalis* relation as a racial one, despite fairly complete isolation.

Junco caniceps dorsalis

Racial characters.—For characters distinguishing *dorsalis* from *J. c. caniceps,* see page 181.

Dorsalis and *J. phaeonotus palliatus* of southern Arizona are not so closely related as was formerly supposed. The distinctness of the two is much more apparent in birds in the flesh than in skins, since coloration of plumage is similar. Interbreeding of the two, which had been assumed from the variable amount of red on the wings of *dorsalis* (a *palliatus* character), has not been found.

Characters of *dorsalis* which differentiate it from *J. phaeonotus palliatus* are dark brown instead of yellow iris, flesh-colored instead of yellow lower mandible, and flesh-colored instead of faintly yellowish feet. The yellow lipochrome which is lacking in these soft parts of *dorsalis* is a constant feature of all forms from Arizona to Central America. In some kinds of birds such pigment is highly variable, but its constancy in the southern juncos seems to mark a major division of the genus.

Other less constant characters that distinguish *dorsalis* from *palliatus* are absence, usually, of red on wings; clearer neutral grays of head, rump, and underparts; slightly darker red of back; longer wing (3 per cent); longer bill (4 to 5 per cent); deeper bill (3 to 7 per cent); and less white in tail (see p. 212). The tail, tarsus, and toes are not significantly longer.

Nongeographical variation.—Dwight was of the opinion (1918, p. 300) that *dorsalis* "... showed a good deal of variations in plumage. . . ." I cannot concur in this, for the coloration of all parts but the wings is as constant as in *J. c. caniceps*. The bearing of the problem of uniformity of *dorsalis* upon its possible hybrid origin calls for a careful analysis of intraracial variation.

Mahogany red areas on the outer webs of the inner secondaries and greater secondary coverts appear in 9 out of 230 *dorsalis* examined, or in 3.9 per cent. This occurrence of a *phaeonotus* character is not so great as that of red pileum in *J. c. caniceps* and is only slightly greater than that of white wing-covert spots in *J. h. hyemalis,* neither of which characters has been thought to point to hybridization in these races. The reddish secondaries, though suggestive of *phaeonotus,* may not be the result of any recent hybridization. The condition is not limited to areas adjacent to the range of *J. phaeonotus palliatus.* Of the 9 individuals displaying red on the wings, 6 were on their breeding ground. One of these was from the Sierra Ancha, nearest point to the range of *palliatus,* three from the White Mountains, a region somewhat more remote from *palliatus* and inhabited by a large population of *dorsalis,* whereas one was from the San Francisco Mountains, northern limit of *dorsalis,* and one from east central New Mexico at the northeastern limit of *dorsalis.*

The same parts of the wing feathers that occasionally are reddish, much more often are bright buff; 21 per cent are so marked. This character occurs in about the same percentages in *caniceps* and is most prevalent in first-year birds and in females.

Red on the pileum occurs in 1.7 per cent, compared with 6.2 per cent in *caniceps* and 1.7 per cent in *palliatus.* White in the wing coverts appears in 0.8 per cent, hence somewhat less frequently than in *caniceps.*

A white basal segment of the culmen is a *caniceps* character, inherited independently of the pigmentation of the remainder of the upper mandible (see p. 188), which occurs in 4.7 per cent of *dorsalis.* Five such birds have been taken in the White and Mogollon mountains and five in the San Francisco Mountains. Thus it is not limited to the regions closest to *caniceps.* Two birds, one a winter specimen, have incomplete black pigment on the upper mandible apart from the culmen. One is type 7 of the Kaibab hybrid series, the other type 6. This latter was breeding in the Mogollon Mountains (Pivot Rock Spring) at the southern border of the range of the race and far removed from *caniceps.* Two breeding birds with comparable hybrid bill patterns were taken in Utah, one 10 miles east of Kamas, and the other at Cedar Breaks. These two *caniceps* and the one *dorsalis* are the only individuals of either race with this intermediate pattern that have been taken outside of the areas where there is interbreeding.

The range of variation in hood color is less than in *caniceps* and the difference in the sexes is lacking. The lower surface of the head is either pale or pallid neutral gray. No geographic correlations could be detected. The red color of the back is highly uniform.

TABLE 4

OCCURRENCE OF RECTRIX PATTERN IN J. C. DORSALIS AND J. C. CANICEPS (IN PERCENTAGES)

	Male		Female	
	dorsalis	*caniceps* (four separate populations)	*dorsalis*	*caniceps* (four separate populations)
Rectrix 4				
Inner web:				
pure black	5	0–7	6	6–17
mixed	95	93–100	94	83–100
Outer web:				
pure black	72	40–57	66	61–70
mixed	28	41–58	34	25–39
pure white	0	2–5	0	0–8
Rectrix 5				
Inner web:				
mixed	79	10–61	80	47–76
pure white	21	39–90	20	24–53
Outer web:				
pure black	1	0	4	0
mixed	80	38–70	81	66–83
pure white	19	30–62	15	17–34
Rectrix 6				
Inner web:				
mixed	6	0–4	14	0–10
pure white	94	96–100	86	90–100
Outer web:				
mixed	7	4–15	34	0–10
pure white	93	85–96	66	90–100

No geographic variation in the white areas of the tail could be found within *dorsalis*, but the individual variation is comparable in range to that in *caniceps*. Pure white outer webs on rectrix 4 are lacking in *dorsalis*, but present in a few *caniceps*. Pure black outer webs on rectrix 5 are present in a few *dorsalis*, but lacking in *caniceps*. Apart from these, the same variants are present in the two forms. The color variants of the inner web of rectrix 4 average the same in occurrence in *dorsalis* and *caniceps*, but the outer web is more often black in *dorsalis* (at least in males) and never is pure white. Rectrix 5 is oftener pure black or mixed on both webs in *dorsalis* than in *caniceps.* Rectrix 6 is not significantly different in the two races, except that females of *dorsalis* show more black. Average sexual difference is found in rectrices 5 and 6 in *dorsalis,* and in rectrices 4 and 5 in *caniceps.* In *dorsalis* all webs of rectrices 4 to 6, except the inner web of 4, show in one sex or the other a greater average amount of black in *dorsalis* than in *caniceps.*

The differences between the average measurements of *dorsalis* (table 5) and those of *caniceps* are given on page 180. All those mentioned are significant statistically, that is, they are five times the probable error of the difference. Coefficients of variability are similar to those for *caniceps,* except for the middle toe, and hence show no evidence of greater heterogeneity in this race that would suggest hybridization. The ranges in value in all size characters overlap to some degree the measurements for *J. c. caniceps.*

TABLE 5

Measurements of J. c. dorsalis

Measurement	Sex	No. of specimens	Mean with prob. error	Standard deviation	Coeff. of var.
Wing...............	♂	95	82.38 ± .15	2.23	2.70
	♀	47	77.81 ± .15	1.53	1.96
Tail...............	♂	87	76.70 ± .19	2.59	3.37
	♀	43	72.74 ± .20	2.02	2.77
Bill length.........	♂	101	8.87 ± .02	0.38	4.34
	♀	48	8.79 ± .04	0.39	4.45
Bill depth..........	♂	98	6.83 ± .02	0.27	3.98
	♀	46	6.70 ± .03	0.31	4.61
Tarsus.............	♂	103	20.85 ± .04	0.60	2.88
	♀	50	20.70 ± .06	0.60	2.89
Middle toe.........	♂	102	11.98 ± .04	0.63	5.25
	♀	49	12.01 ± .05	0.53	4.44
Hind toe...........	♂	87	8.47 ± .03	0.48	5.63
	♀	51	8.27 ± .05	0.50	6.02

Coefficients of correlation are: wing and tail, .721 ± .035; tarsus and middle toe, .287 ± .058.

Geographical variations within the race.—*Dorsalis* seems devoid of any internal variations correlated with geography. Characters of forms to the north and to the south, when present in *dorsalis,* are not confined to marginal areas (see p. 206).

Distribution in breeding season.—There is a large area in the Mogollon Mountains of Arizona and New Mexico over which distribution is nearly continuous. In addition to this, numerous isolated mountain ranges are occupied, much as in the breeding range of *J. c. caniceps.* Plant associations in which *dorsalis* breeds consist of coniferous forests wherein the following types predominate: *Pinus ponderosa, Abies,* and, less commonly, *Pseudotsuga.* Birds also breed in pure groves of aspens and in coniferous forests with some oaks intermixed. Compared with the habitats of *J. c. caniceps,* those in which I have found *dorsalis* are, if anything, less arid, more luxuriant forests, although occasionally birds will breed in the dry lower portions of the yellow pine belt. Ground cover is rarely as poor in grass, low bushes, and humus as in many parts of the range of *J. c. caniceps* in Utah and Nevada. However, the presence of good stands of yellow pine in the Transition Zone provide junco habitat at lower zonal levels than in Utah and Colorado.

New Mexico.—Occurs chiefly in high Transition and Canadian zones (Bailey, 1928, p. 740), above 7000 feet, between latitudes 32° and 35°, in the central and southern parts of the state. The following mountains are included: Capitan, Sierra Blanca, Sacramento, Guadalupe, Datil (probably), Magdalena, San Mateo of Socorro County (probably), Black Range, Mimbres, Pinos Altos, and the Mogollon group of Catron County. A single *dorsalis* is at hand from the San Mateo Mountains of Valencia County. Since the Zuni Mountains at the same latitude have a hybrid population, such may also be the condition in the San Mateo Mountains. Sight records from Colfax County (Bailey, *loc. cit.*) are not substantiated by specimens and doubtless pertain to *J. c. caniceps*, which is known to breed there.

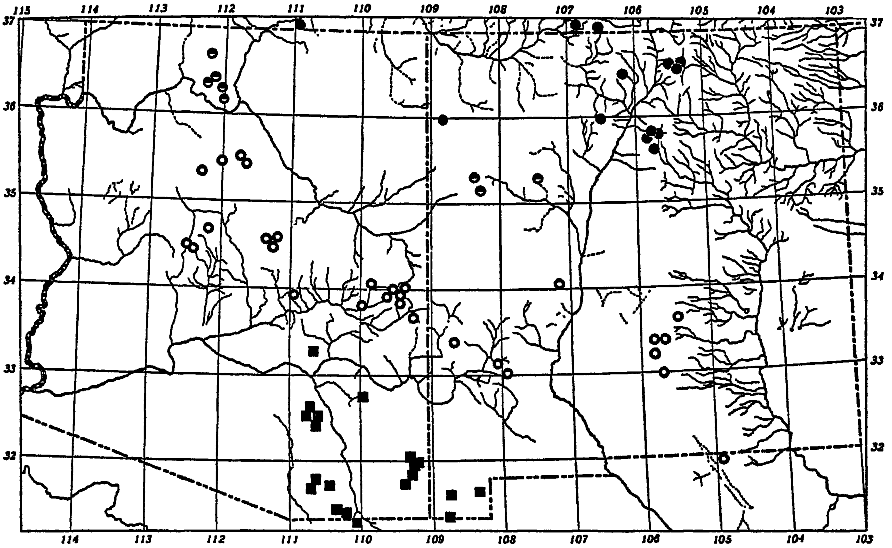

Fig. 5. Distribution of breeding or permanently resident juncos in Arizona and New Mexico. Each symbol represents a locality from which specimens have been examined. Dots, *J. c. caniceps;* circles, *J. c. dorsalis;* half dots, intermediates between *J. c. caniceps* and *J. c. dorsalis;* squares, *J. p. palliatus.*

Texas.—Known only from the Guadalupe Mountains, Culberson County, just south of the New Mexico line. A juvenile taken here by V. Bailey, August 11, 1901, indicates breeding. Such migration as does occur in *dorsalis* does not begin until September, after the postjuvenal molt is finished.

Arizona.—Occurs in high Transition and Boreal zones (Swarth, 1914, p. 93, map) in mountains south of the Colorado and Little Colorado rivers and north of the Gila River (except Pinal Mountain in Gila County). This includes the mountains of the Mogollon group from Baker's Butte, southeast through the White Mountains into New Mexico, and the Sierra Ancha. It also includes much of the Coconino Plateau from Bill Williams Mountain east to the San Francisco Peaks and north, irregularly, to the south rim of the Grand Canyon. Also breeds on Mingus Mountain and on the mountains near Prescott.

Distribution in winter.—Winters on the breeding grounds and at lower elevations in the mountains within the breeding range. Few individuals stray south of the southern limits of the breeding range of the race. Several winter records to the southward have been based upon *caniceps–dorsalis* intermediates or upon birds incorrectly identified. From the Chircahua Mountains, Arizona, a single January-taken bird is at hand. This is in contrast to 58 *J. c. caniceps* taken from the same locality in winter. Other unequivocal winter or migration records based on specimens taken south of the breeding range are: Big Hatchet Mountains, Hidalgo County, New Mexico (1), May 18, 1892; Playa, Hidalgo County, New Mexico (1), February 17, 1885; "southwestern New Mexico" (1), November 5, 1873; Chisos Mountains, Texas (1), January 28, 1914; Huachuca Mountains, Cochise County, Arizona (1), January 7, 1905; and Pinal County [=Santa Catalina Mountains], Arizona (2), October 26, 1884, and February 11, 1886. Reports of *dorsalis* in Chihuahua and northeastern Sonora by Ridgway (1901, p. 298) apparently were based on skins in the American Museum. In Allen's report (1893, p. 39) covering this matter, only one *dorsalis* from San Diego, Chihuahua, is mentioned. The only junco now at the American Museum from San Diego is no. 56861, which is *J. c. caniceps;* no *caniceps* from this locality was recorded by Allen. Records south of the United States border therefore are lacking. That the race occasionally ranges south of the line is not improbable in view of occurrences in the Huachuca Mountains and other ranges along the Mexican boundary.

Relationships with adjacent forms: J. c. caniceps (see p. 186), *J. phaeonotus palliatus.*—The only important character of *palliatus* which occurs in *dorsalis* is the red on the wing. This has been shown to be variable, and when occurring in *dorsalis* it is not limited to regions adjacent to *palliatus. Palliatus* occasionally may lack this red. I have never seen evidence of intermediacy in the striking character of yellow iris and yellow lower mandible of adult *palliatus.* No intermediate or mixed populations are known, nor is it apparent where they might occur. The closest points of approach of the ranges of the two forms in southeastern New Mexico are the Animas Mountains and the mountains near Silver City. Sixty miles of Lower Sonoran desert intervenes and the total distance is probably about 90 miles.

In Arizona from the top of the Sierra Ancha where I was collecting breeding *dorsalis,* Pinal Mountain, 37 miles to the south, could be seen, where *palliatus* in pure form had been taken the week before. Between lay the Salt River Valley. This is the closest point of approach known, although the distance is not much greater along the Gila River Valley to the southeast. Pinal Mountain is the northernmost outpost of the yellow-eyed juncos, which in various forms extend south to Panama. This 37-mile break in distribution is one of great significance; it divides the genus into two major groups, geographically complementary, between which there is at present no interbreeding.

Rassenkreis **Junco phaeonotus**
Mexican Junco

This group consists of two geographic differentiates, *J. p. palliatus* in the north and *J. p. phaeonotus* in the south. Between them is an extensive gradient which occupies a great part of central Mexico along the Sierra Madre

Occidental. It follows that sharp interracial boundaries do not exist, either geographically or morphologically. The rassenkreis occupies the mountains of southeastern Arizona, extreme southwestern New Mexico, and Mexico south to the Gulf of Tehuantepec. There is no migration.

Principal characters of the group.—Iris yellow; lower mandible pale yellow; upper mandible black. Back area reddish brown (Kaiser brown to hazel), sharply defined anteriorly and posteriorly with lateral margins more or less confluent with reddish areas of wing coverts and inner secondaries; reddish color produced by phaeomelanins, as in *J. caniceps* and *J. bairdi;* eumelanin practically or entirely absent from the area; tips of feathers grayish because of lack of phaeomelanin. Lores and ocular region black, contrasting with grays of head. Sides smoke gray to buffy brown and snuff brown, but not sharply set off from pale smoke gray of breast and throat. Side color produced by combination of terminal eumelanin and proximal deposits of phaeomelanin in barbules. Tail with two, rarely three, outer feathers partly white. Size moderately large, weight 19.1 gm. average; wing of males averaging 77 to 79 mm.; feet fairly large.

Sexual differentiation in coloration is nearly lacking. Females display slightly more phaeomelanin in the sides and on the rump. The heads of females are not lighter than those of males. The amount of black on the fifth rectrix averages greater in females. Size differentiation in wing and tail is about 5 per cent, as in *Junco caniceps;* but unlike *caniceps* and *J. alticola, phaeonotus* shows no sexual dimorphism in bill and tarsus and apparently none in the toes. An immature plumage is not distinguishable.

The effect of wear upon the reddish areas is the same as in *Junco caniceps.* The smoke gray and even the buffy browns of the sides are greatly reduced by wear and fading in the course of the year. The color of the head and breast is not altered greatly, except that it becomes slightly darker through staining and exposure of the basal parts of the feathers late in the breeding season.

Junco phaeonotus palliatus

Racial characters.—*Palliatus* and *J. p. phaeonotus,* at the geographic extremes, are constantly differentiated by the darker grays and buffs in the plumage of the latter. In *J. p. palliatus* the anterior upper parts are pale mouse gray rather than mouse gray; rump light grayish olive rather than deep olive; sides smoke gray rather than buffy brown. Less constant characters are slightly lighter gray of breast, greater amount of white on fifth rectrix, more frequent white spotting of fourth rectrix and less prevalent black spotting of sixth, and paler, less abundant phaeomelanin in the barbules of the back, producing a lighter red-brown than in *J. p. phaeonotus.* Extreme populations of *palliatus* are on the average longer winged (2 per cent), longer tailed (2 per cent), longer billed (4–5 per cent), and have longer middle toes (2 per cent) and shorter tarsi (2 per cent) than *J. p. phaeonotus.*

For differences between *palliatus* and *J. c. dorsalis* see page 205.

Nongeographical variation.—Red on the crown occurs in 1.7 per cent of 400 individuals, the same as in *dorsalis.* Occurrence of white wing coverts in but 0.5 per cent is likewise similar to *dorsalis*. There is no red on the wing coverts in 1.5 per cent; all birds lacking red were from the Pinal, Chiricahua, and Santa Catalina mountains. Even so, I hesitate to consider it geographically limited to these areas, for with a character of so infrequent occurrence extremely large samples would be necessary to prove its absence. In addition to individuals that are entirely lacking in red, certain ones have the color reduced so that it involves only one or two secondary coverts. Such individuals occur in Chihuahua as well as in Arizona. The red never occurs on more than the greater secondary coverts and on the three innermost secondaries. No birds were found with white base of the culmen, such as occurs in 4.7 per cent of *dorsalis*. This would point to the origin of this feature in *dorsalis* from *J. c. caniceps*.

TABLE 6

OCCURRENCE OF RECTRIX PATTERN IN J. P. PHAEONOTUS, J. P. PALLIATUS AND J. C. DORSALIS

	Male			Female		
	J. p. phaeonotus	*palliatus*	*dorsalis*	*J. p. phaeonotus*	*palliatus*	*dorsalis*
Rectrix 4						
Inner web:						
pure black	83	33	5	80	51	6
mixed	17	67	95	20	39	94
Outer web:						
pure black	100	95	72	100	97	66
mixed	0	5	28	0	3	34
Rectrix 5 (always mixed in *J. phaeonotus*)						
Inner web:						
⅛ or less black	10	59	(21 pure white)	8	27	(20 pure white)
⅛ or less white	59	7		80	23	
Outer web:						
pure black	98	47	1	100	69	4
trace of white	2	27	(19 pure white)	0	21	(15 pure white)
mixed	0	26	80	0	10	81
Rectrix 6						
Inner web:						
mixed, or trace of black	93	84	6	96	86	14
pure white	7	16	94	4	14	86
Outer web:						
mixed, or trace of black	93	76	7	100	77	34
pure white	7	24	93	0	23	66

The tone of gray on head, rump, and sides varies within narrow limits in any one population; the important variations in these features are geographically correlated.

No geographic variation in white of tail within the Arizona area was detected. In *J. p. phaeonotus, palliatus,* and *J. c. dorsalis* successively greater amounts of white occur in each web of all three feathers. The difference is much greater in each instance than it is between *caniceps* and *dorsalis.* Pure white vanes on rectrix 5 are lacking in *J. phaeonotus; only J. p. phaeonotus* lacks mixed as well as white variants of the outer webs of rectrices 4 and 5. Sexual differences are pronounced in both vanes of rectrix 5 in all three forms. It also is distinct in the inner vane of 4 in *palliatus* and in rectrix 6 in *dorsalis.*

The significant differences between the average measurements and those for *dorsalis* are given on page 206. Variability of wing is 7 to 18 per cent higher than in the rassenkreis *caniceps,* approaching the degree of variability found in the tail. This is not the result of assembling birds from different mountain ranges for statistical treatment, for a similar variability was found in each locality. No increase in tail variation occurs, at least in males. Bill depth is 6 to 8 per cent more variable; the middle toe is 10 per cent more variable than in *caniceps,* but is similar to *dorsalis.* Other characters have similar coefficients of variability. The occurrence of increased variability in mensurable characters is interesting in a race in which plumage variation is relatively slight. Intraracial correlation of characters is essentially the same as in *Junco caniceps.*

TABLE 7

Measurements of J. p. palliatus of Arizona

Measurement	Sex	No. of specimens	Mean with prob. error	Standard deviation	Coeff. of var.
Wing.............	♂	113	79.34 ± .14	2.28	2.87
	♀	78	75.47 ± .15	1.92	2.54
Tail..............	♂	111	75.16 ± .15	2.39	3.17
	♀	71	72.17 ± .18	2.22	3.07
Bill length.........	♂	105	8.43 ± .02	.36	4.27
	♀	59	8.50 ± .03	.40	4.70
Bill depth..........	♂	89	6.33 ± .02	.32	5.05
	♀	52	6.47 ± .03	.32	4.94
Tarsus............	♂	117	20.94 ± .03	.57	2.72
	♀	77	20.95 ± .04	.57	2.72
Middle toe.........	♂	111	12.06 ± .03	.52	4.31
	♀	76	11.86 ± .04	.52	4.38
Hind toe...........	♂	114	8.55 ± .03	.41	4.78
	♀	78	8.44 ± .04	.48	5.68

Geographical variation in Arizona.—Since the gradient between *palliatus* and *J. p. phaeonotus* will be considered at length, there remain to be mentioned here only such variations as have been detected within the range in Arizona and New Mexico. Large series from the Chiricahua and Huachuca ranges in Arizona were compared. The Huachuca group had bills 3 per cent longer and deeper. This difference is reliable statistically and occurs in both males and females. These two isolated colonies are otherwise similar except for a small difference in wing length. Comparable differences may exist between groups from other of the mountain ranges, but the samples are not large enough to permit establishment of small average differences.

Distribution.—In the absence of any evidence for migration, records of occurrence for all months of the year are used to indicate range. Areas in New Mexico, Arizona, Sonora, and Chihuahua are included, for despite the beginning of a gradient in Chihuahua toward *phaconotus,* the resemblance of these northern Mexican populations is close to the Arizona extreme.

Palliatus is restricted chiefly to isolated mountain peaks and ranges in Arizona and to the Sierra Madre in Chihuahua and Sonora. It occurs in the pine association, Transition Zone (Nelson and Goldman, 1926, p. 585), usually above 7000 feet, but occasionally as low as 6000 feet. There is a winter record at 4000 feet, below the pine belt, for the Santa Catalina Mountains of Arizona. The pine association may have a considerable mixture of deciduous oak. Prominent forest associates are *Pinus ponderosa* var., *Pinus chihuahuana, Pseudotsuga taxifolia,* and *Abies religiosa.* The forest floor which the junco occupies, though perhaps more arid on the average than that in the range of *dorsalis,* usually consists of pine needles and oak leaves, with some green bushes such as *Symphoricarpos, Garrya, Rhus, Ceanothus,* and brake ferns.

New Mexico.—Found in the Animas, San Luis, and Big Hatchet mountains of the extreme southwestern section of the state.

Arizona.—Occurs on the Graham, Chiricahua, Santa Catalina, Santa Rita, Whetstone, and Huachuca mountains in the region south of the Gila River. Occurs on Pinal Mountain north of the river.

Sonora.—Known from the San José Mountains just southeast of the Huachuca Mountains of Arizona. Almost certainly to be found along the west slopes of the Sierra Madre.

Chihuahua.—Occurs in the pine belt of the Sierra Madre from at least latitude 30° 15′ to the southern end of the state. Also occurs in the San Luis Mountains just south of the United States boundary.

Intergradation between palliatus and J. p. phaeonotus.—The changes in characters along the north–south mountain ranges of Mexico are gradual, beginning in Chihuahua and terminating in the opposite extreme south of the Rio Grande de Santiago in Jalisco. The Mexican material has not been assembled at one place for examination. This circumstance and the fact that the specimens often are not seasonally comparable have made detailed analysis difficult. Accordingly, the changes in the coloration of the three important body areas, rump, crown, and flanks, cannot be analyzed separately. It was evident in studying the intermediates that variation in these three areas did not correlate, various shades of browns and grays in these regions being combined on the same bird.

Each bird was classed according to the total color effect: (1) typical *palliatus;* (2) slightly darker and browner; (3) intermediate; (4) slightly paler than *J. p. phaeonotus;* (5) typical *J. p. phaeonotus.* The Arizona populations are composed chiefly of type 1, with less than 10 per cent of type 2 and none any darker. Mexican birds south of the Rio Grande de Santiago and the Rio Pánuco are of type 5, except for 11 per cent of type 4.

Mensurable characters which show statistically significant differences between extremes are wing, tail, bill length, and middle toe. In the intervening area a progressive alteration is to be noted. Tarsal length changes significantly, but it is not importantly different at the two geographic extremes. The white areas of the tail show pronounced change, almost entirely in the northern section of the intergradational area.

Chihuahua region.—Out of ten birds from localities close to latitude 30° in the Sierra Madre, two are of type 2, the remainder of type 1. A group of breeding birds in worn plumage from Pinos Altos near latitude 28° were not noticeably different. However, a group of 18 fresh-plumaged birds from the same vicinity (30 miles west of Miñaca) showed plainly an increase in the darker plumage types, with types 3 and 4 appearing for the first time.

TABLE 8

OCCURRENCE OF PLUMAGE TYPES IN INTERGRADES

Locality	Type				
	1	2	3	4	5
Chihuahua (lat. 30°)................	8	2	0	0	0
Chihuahua (lat. 28°), fresh plumages..	10	5	2	1	0
Coahuila-Durango..................	3	5	3	1	0
Tamaulipas–northern Jalisco.........	1	5	11	27	10
Mexico south of Rio Grande de Santiago and Rio Pánuco.............	0	0	0	9	80

Wing and tail diminish in average values in the Chihuahua group in both males and females. All birds from localities between 28° and 30° have been combined in these averages. The diminution is no greater than the slight colonial differentiation between the Huachuca and Chiricahua groups, but it is significant as a step in differentiation toward *phaeonotus*. Middle toe length diminishes to a point halfway between the extremes; bill length remains the same as in the Chiricahua Mountains. The tarsus is remarkably short, reaching a figure distinctly lower than in either extreme type. This is a case of local differentiation unrelated to other geographic trends. I do not think it is the result of interbreeding of the two extremes, as no similar tendency is seen in intergrades in Durango, Coahuila, and Zacatecas. It would seem to be a case of colonial differentiation, extremely significant as a possible step toward local racial evolution.

The white in the tail is diminished in Chihuahua to essentially the same value as in southern Mexico. The graph (fig. 6) indicates the increase in black areas on the outer tail feathers of males, the same individuals as those for which size characters were determined.

Coahuila-Durango region.—Twelve birds from scattered localities in the Sierra Madre of Durango and the mountains of southern Coahuila are as predominantly of intermediate type as any sample at hand. Few extreme pale types appear, although the mean of the group is still closest to *palliatus*. The sample is not adequate for analysis of size characters, as averages would be unreliable where such small differences are involved.

Tamaulipas-Tepic region.—Included in this group are birds from many localities in the Sierra Madre Occidental and Sierra Madre Oriental, as also some from mountains in the intervening plateau of this section. All localities in Tamaulipas, Nuevo León, San Luis Potosí, Aguascalientes, Zacatecas, and Tepic are included, and those in Jalisco north of the Rio Santiago.

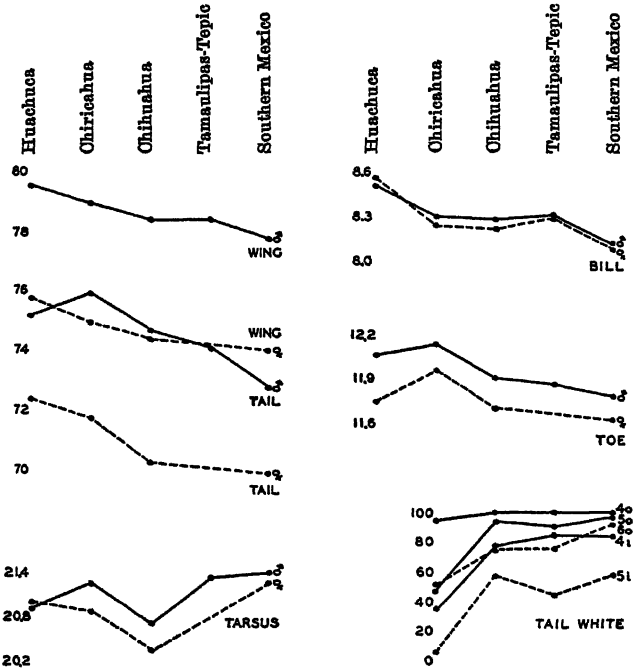

Fig. 6. Intergradation of *J. p. palliatus* and *J. p. phaeonotus.* Average measurements (mm.) of populations (see text for numbers of specimens used). Tail white represented as percentage of occurrence of variants in males of each population: number represents rectrix; *i*, inner web; *o*, outer web; *4i*, *4o*, *5o*, pure black; *6o*, mixed rather than black; *5i*, two-thirds or more black. First vertical series of dots for tail white represents all *palliatus* from Arizona.

Although all color types are found in the assemblage of 54 birds, for the first time types 4 and 5 predominate. An excellent group of 12 fresh-plumaged birds from western San Luis Potosí (Jesús María) are nearly all of type 4 and only one is a typical *phaeonotus.* Other groups, those from the Sierra Nayarit and Zacatecas and from the Sierra Madre Oriental, are more diverse, but average about the same. Even though the average coloration has shifted so as to be closer to *phaeonotus* in passing south from Durango, it should be emphasized that no more change in character is involved than between this group and the southernmost group constituting typical *phaeonotus.*

The size characters are similar to those of the Chihuahua group. The curves for wing and tail (fig. 6) level out between Chihuahua and this region. Bill maintains a value similar to that in the Chihuahua and Chiricahua groups, and middle toe drops but slightly. Tarsus is greatly increased over the peculiarly low Chihuahua average and is even higher than in the Chiricahua group. Thus in the size characters which show a gradient from one extreme to the other, there are no sharp breaks in the curve between this region and Chihuahua, and there is usually a tendency to remain constant. White in the tail remains about the same as in Chihuahua.

Region south of the Rio Grande de Santiago and the Rio Pánuco.—Within this large terminal area, which extends south to the limit of the rassenkreis in Oaxaca, no major changes in coloration or size occur. The rivers along the north of this area form convenient lines of demarcation and to a degree represent barriers in distribution to the northward. However, the break in distribution is no greater than between many mountains within this and other regions.

Color types 1, 2, and 3 are lacking. Type 4 occurs in only about 11 per cent, so that these populations are as uniform in color type as are the Arizona birds at the opposite extreme.

The curves representing size show distinct breaks between this region and the one next north with respect to wing, tail (at least of males), and bill lengths. Change in tarsus and middle toe are slight but continue trends of geographic variation already manifested farther north. The differences in wing, tail, and bill are no greater than between Arizona and Chihuahua or than between the Chiricahua and Huachuca mountains, but they are distinctly greater than between Chihuahua and Tamaulipas-Tepic. Tail white is not materially different.

Summary.—In the three intermediate geographic groups variation in color increases slightly compared with that at the geographic extremes. Variation in color of different parts of the body is not closely correlated in individuals, but is correlated as between populations. Change in average coloration is not abrupt between any two of the regions and constitutes an even gradient between extremes. Shift in average from a value closest to *palliatus* to one closest to *J. p. phaeonotus* occurs between Durango and Zacatecas (and neighboring states). The point marked by this shift, although possibly useful as a purely arbitrary boundary of races, is actually of no more biological significance than any of the other points along the gradient.

Length of wing, tail, and bill grade off to the southward with two principal breaks, one between Arizona and Chihuahua and the other between Tamaulipas-Tepic and the southernmost area. Tarsus shows peculiar local differentiation unrelated to the general geographic trend. It is therefore patent that although the color gradient is more or less uniform, the size gradient is more erratic, with subterminal breaks. The averages for tail markings show a single break, which, relative to the color gradient, is far north. Average changes along the cordillera are not effected in unison. Any nomenclatural treatment of these groups of intergrades would necessarily be extremely artificial.

Junco phaeonotus phaeonotus

Racial characters.—For characters distinguishing *J. p. phaeonotus* from *palliatus* see page 211.

A number of constant, strongly marked features distinguish *J. p. phaeo-*

notus from *Junco fulvescens* of central interior Chiapas. There is no point of contact between these forms. The southernmost point at which *J. p. phaeonotus* occurs in Oaxaca is 200 miles distant from the range of *fulvescens*, between which lie the extensive lowlands of the Isthmus of Tehauntepec. This is a greater interruption in the distribution of the genus than is found anywhere to the north on the mainland of North America. The back of *fulvescens* is raw umber rather than Kaiser brown, owing to a different type of pigment mixture (see p. 226). This color is confluent with the olive brown of the rump, so that the reddish brown of the back is sharply defined only anteriorly. The sides are Sayal brown rather than buffy brown. Most striking is the heavy bill of *fulvescens*, which is 20 per cent deeper, with practically no overlap in individual variation with *phaeonotus*. Bill length is 6 to 9 per cent greater, tarsus 1 to 2 per cent greater, and the toes 4 to 10 per cent greater in *fulvescens*. Wing is 6 per cent shorter and tail 7 per cent shorter than in *J. p. phaeonotus*. Tail white is somewhat less extensive on the average on rectrices 5 and 6. The difference in proportions between *fulvescens* and the *J. phaeonotus* rassenkreis is more marked than between the rassenkreise *J. oreganus* and *J. caniceps*, or *J. caniceps* and *J. phaeonotus*, or *J. oreganus* and *J. hyemalis*.

TABLE 9

MEASUREMENTS OF SOUTHERN MEXICAN J. P. PHAEONOTUS

Measurement	Sex	No. of specimens	Mean with prob. error	Standard deviation	Coeff. of var.
Wing..............	♂	56	77.67 ± .20	2.27	2.92
	♀	25	73.97 ± .29	2.17	2.93
Tail..............	♂	49	72.66 ± .23	2 44	3.36
	♀	25	69.86 ± .38	2.79	3.99
Bill length.........	♂	58	8.10 ± .03	0.37	4.56
	♀	25	8.08 ± .04	0.33	4.04
Bill depth..........	♂	50	6.19 ± .04	0.38	6.13
	♀	23	6.12 ± .04	0.30	4 98
Tarsus.............	♂	59	21.36 ± .05	0.57	2.66
	♀	26	21.25 ± .09	0.71	3.36
Middle toe.........	♂	52	11.78 ± .05	0.49	4.15
	♀	25	11.63 ± .06	0.43	3.71
Hind toe...........	♂	62	8.47 ± .03	0.41	4.84
	♀	26	8.36 ± .04	0.38	3.51

Nongeographical variation.—There is a notable absence of striking plumage variations, compared with northern forms. Only one occurrence of red pileum and none of absence of red on wings or of white basal segment of culmen was found. One individual with whitish margins of the wing coverts was noted, but the margins hardly compare with the distinct white spots occasionally found in *J. caniceps* and other northern groups. Plumage variations, aside from the tail, are confined to lesser differences in tones of grays and hues of reddish browns and buffs.

Variation in the white of the tail is detailed on page 212.

Coefficients of variability are similar to those for *palliatus*. This means that the comparatively high variability of wing, bill depth, and middle toe is maintained in this member of the rassenkreis. No evidence of a different system of intraracial correlation of characters was detected.

Geographical variation.—No thoroughly conclusive evidence of variation of this sort in southern Mexico could be found. The series from restricted regions were not adequate to demonstrate colonial differentiation in dimensions. Material available from Vera Cruz suggests that birds from that region may be slightly shorter winged than those from the vicinity of Mexico City.

Van Rossem (1938, pp. 132–133) has described two races in southwestern Mexico from within the range of *J. p. phaeonotus* as here defined. These were based on very small series of adults in the British Museum. The same material had been studied by me and some notes taken on it in 1934. With our present knowledge of the types of variation in the genus *Junco,* it should be apparent that a conclusion concerning inherent differences in populations could not be safely reached on the basis of samples of from 5 to 7 adult individuals. Certainly if slight colonial differentiation is represented by these described forms, their equivalence to other races of junco is not apparent either in degree of differentiation or in certainty of the characters ascribed.

Junco phaeonotus colimae was described from 7 specimens from the Sierra Nevada de Colima, Jalisco. This is at the western end of the highlands of southern Mexico. The characters given are: "entire coloration decidedly darker and flanks browner." In studying this material I had recorded, as with all the *phaeonotus* complex, the general depth of coloration gained from inspection of several sections of the plumage (see p. 214). Particular attention was always paid to the flanks where in unworn plumage, as in this series of seven, the dark brown of *phaeonotus* shows to particular advantage. There is an appreciable seasonal alteration in the tones of the grays and browns in this species which had become apparent to me earlier in surveying the Mexican collections in American museums, and this was taken into account in classifying the types of coloration. Five of the 7 skins in question, including the type, were recorded by me as of average *J. p. phaeonotus* coloration, that is, of color type 5 (see p. 212); 2 were marked lighter than average *J. p. phaeonotus,* toward *palliatus,* or type 4. Thus I am unable to confirm even a minor differentiation in the Sierra Nevada de Colima or in specimens from Juanacatlan from the same section of the state of Jalisco.

Junco phaeonotus australis was described from the Sierra Madre of Guerrero, which is isolated from the main range of *J. p. phaeonotus* to the north by about 80 miles of unsuitable country. The characters ascribed are "upper parts brighter [than *J. p. phaeonotus*] and more extensively red, particularly on tertials and lower back; underparts more brownish-gray, particularly on flanks; bill decidedly larger and wing and tail shorter." Only 5 adults were available and but 3 of these were sexed. The birds are worn specimens taken in July and August. My own notations characterize all as typical *J. p. phaeonotus.* Duskier underparts and more prominent red on back and wings are features which become enhanced in worn plumage, and the extent of red is decidedly variable individually. Study of the distribution of the red would certainly be worth while in a larger series in fresh plumage. I was not impressed by any abnormal aspect of this pigment in my handling of the series. The 3 sexed birds were males, and 2 of these showed such wear in wing and tail that I felt measurement of the feathers would be misleading. My measurements of the one less-worn male are: wing, 76 mm.; tail, 72. This and van Rossem's measurements (wing, 70–77, and tail, 65–71) do not fall outside the curve of variation represented by the standard deviation for males and females of *J. p. phaeonotus* (see table 9, p. 218). (The 2 unsexed birds included by van Rossem may have been females.) They are lower than average, but a trend toward short wing and tail is in no sense proved statistically and is not even as clearly indicated as in the birds of Vera Cruz. Bill measurements, because not taken in comparable fashion by different workers, cannot be compared. My only measurement of a sexed bird was 8.6 for bill length; depth was not taken because the mandible was out of place. The length measurement is above average for *phaeonotus* but is exceeded by measurements of a number of individuals from the vicinity of the valley of Mexico. The only safe conclusion regarding dimensions is that differentiation in the Guerrero area is not yet demonstrable. We must have much better grounds than now available before differentiation of racial magnitude can be ascribed to the Guerrero population, even though the probabilities are good that there is a minor colonial differentiation there.

Distribution.—Permanent resident, in typical form, in the higher mountains on and surrounding the southern end of the Mexican Plateau, south of the Rio Grande de Santiago and Rio Pánuco, and including the highlands of Guerrero and Oaxaca. (For intergradient regions see p. 215.) The race occurs in pine or other coniferous forests of the Transition and Boreal zones, from 8000 feet to timber line (occasionally 14,000 feet). Some stations of record are apparently somewhat below 8000 feet. Prominent forest trees are *Pinus montezumae, Pinus liophylla, Abies religiosa,* and species of *Quercus.*

Known regions of occurrence include the mountains of central western Vera Cruz, central Puebla, Tlaxcala, southern Hidalgo, southern and eastern Mexico, central and western Michoacán, southern Jalisco, central Guerrero, and central Oaxaca to Zempoaltepec. Probably occurs in Morelos, extreme northern Hidalgo, Querétaro and Guanajuato.

Relationships with adjacent forms: J. p. palliatus (see p. 215). *J. fulvescens.*—No interbreeding with this form occurs, owing to wide separation geographically. There is no structural intergradation. For further discus sion see pages 218 and 226.

Junco bairdi

Baird Junco

This species is fully isolated from all other juncos in the mountains of the Cape district of Lower California. Its affinities are not with the juncos of northern Lower California, but with the yellow-eyed forms of Mexico and Guatemala. Several important features point to this relation: lack of distinct hood demarcation; back color confluent with that of rump (*alticola* and *fulvescens*), inner secondaries, and coverts; proportions of wing and tail; relatively large bill; and reduced tail white. It possesses several peculiarities of color and proportion that sharply set it off from all others, yet, speaking broadly, it is a pale, dwarfed representative of the Central American juncos. Its range is probably as small as that of any other junco except *insularis* and possibly *vulcani.*

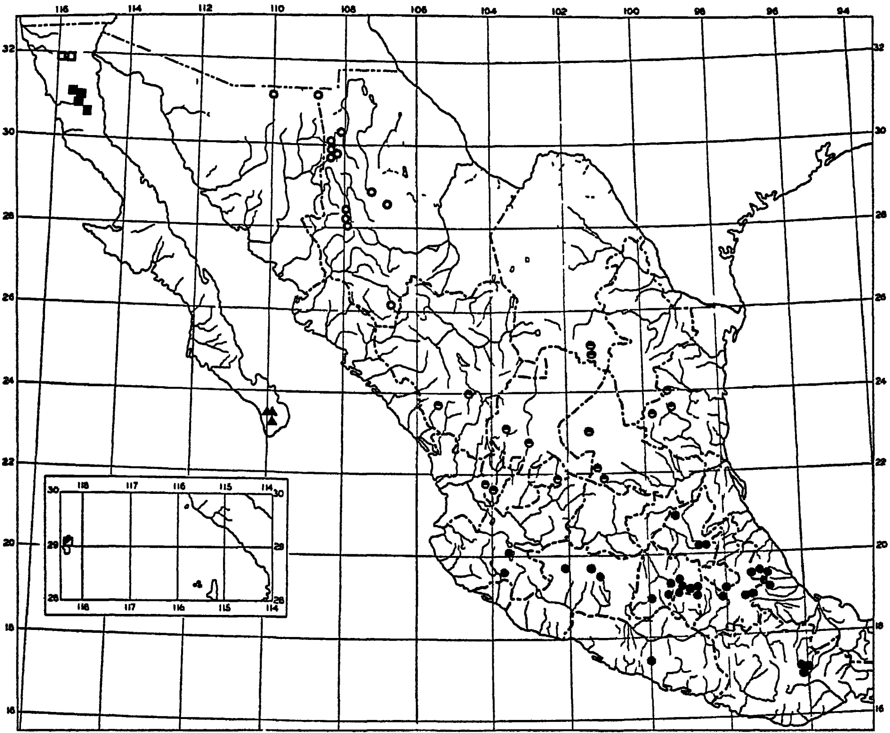

Fig. 7. Distribution of permanently resident juncos in Mexico northwest of the Gulf of Tehuantepec. Each symbol represents a locality from which specimens have been examined. Circles, *J. p. palliatus;* dots, *J. p. phaeonotus;* half dots, distinctly intermediate groups between *J. p. palliatus* and *J. p. phaeonotus* (see text); open squares, *J. o. pontilis;* solid squares, *J. o. townsendi;* solid triangle in square, *J. insularis;* triangles, *J. bairdi.*

Principal characters of the species.—Iris yellow; lower mandible pale yellow; upper mandible brown. Back cinnamon brown, the result of a pale yellowish phaeomelanin unaccompanied by tips of eumelanin on the barbules. This pigmentation might be related either to that of *J. phaeonotus,* which is similar but has a ruddier phaeomelanin, or to that of *fulvescens,* which has the same yellow phaeomelanin but also a peculiar scattered eumelanin which adds a faint olive hue. The cinnamon brown is almost the same as the color found in certain hybrids between *thurberi* and *caniceps* wherein eumelanin is lacking and the phaeomelanin is yellow (see p. 194). This likeness, although possibly identical genetically, does not mean that there is any immediate relationship.

Cinnamon brown confluent with similarly colored margins of inner secondaries and greater secondary coverts, and with buffy brown of rump. Lores dull black, but ocular region and pileum nearly uniform gray (light mouse to smoke gray). Throat and breast pale mouse gray confluent with gray of auricular region. Sides cinnamon, with color extending far forward onto breast, though without a definite line of demarcation with the gray; cinnamon sometimes meets across breast and spreads onto tips of feathers of throat. Color produced by a pure light yellowish phaeomelanin without any trace of the eumelanin found in *fulvescens*. Tail with two outer feathers partly, the outer often completely, white. A third feather (number 4) often with a white spot. Wing and tail short, wing of males averaging 71 mm., and tail 66 mm. Bill and feet moderately large, proportionately. Body size small, weight averaging 17.70 gr. in males, compared with 19.10 gr. in *palliatus* and 18.83 gr. in *townsendi*.

Sexual dimorphism is limited to size and tail pattern. Wing and tail show the usual 5-per cent differentiation. Bill and feet are differentiated to the extent of 1 to 2½ per cent, but none of these differences is entirely reliable statistically. The situation is comparable to that in *Junco phaeonotus,* where dimorphism in bill and feet is entirely lacking or is so slight as to be uncertain statistically. (See p. 224 for tail pattern.)

Wear lightens the cinnamon brown of the back, making it more yellowish, and may entirely remove the cinnamon edgings on the wing feathers. The cinnamon of the sides becomes yellower, less pinkish.

Differential characters.—Bairdi differs from *J. phaeonotus* subsp. most importantly in the extensive cinnamon sides that are devoid of eumelanin, in the lighter, duller cinnamon brown, rather than Kaiser brown or hazel of the back, in the confluency of back and rump colors rather than fairly sharp demarcation, and in shorter wing (9 to 11 per cent), tail (9 to 11 per cent), and tarsus (3 to 5 per cent). Other measurements are very close to the measurements of *J. p. phaeonotus,* while the grays of the head and breast are closely similar to those of *palliatus*. The white of the tail is perhaps closer to that of *palliatus* in total amount, but details of the pattern are, on the average, different (see p. 223).

In view of certain similarities with more southern forms, particularly *fulvescens,* points of difference with the latter may be noted: back of *bairdi* cinnamon brown rather than raw umber (fresh plumage); sides without eumelanin, hence pure cinnamon; pileum light mouse gray rather than dark olive gray; bill 5 to 7 per cent shorter, bill depth 20 per cent less, tarsus 7 per cent shorter; middle toe 5 to 8 per cent shorter; hind toe 7 to 11 per cent shorter. These differences in proportions I consider more important than the differences in color and in wing and tail length between *J. phaeonotus* and *bairdi,* since some of them show no overlapping. The resemblance in side color, throat color, and lower back of *fulvescens* and *bairdi* may be due to parallel lightening and brightening of pigments under comparable, though not identical, environmental influences (selection), and it does not certainly point to immediate relationships.

Bairdi differs so markedly from *insularis* and *townsendi* in the fundamental matters of eye and bill color and hood and back markings as to make detailed comparisons unnecessary. These northern forms are clearly related to the Oregon juncos (including *mearnsi*) and hence belong in a different section of the genus.

Nongeographical variation.—The plumage of *bairdi* is highly uniform. At least three-fourths of all birds have a buff patch on the nape suggestive of a comparable variant in *alticola* but not like the reddish crown of *J. phaeonotus*. This may be even more prevalent in *bairdi* than has been indicated, as some spring birds could have lost this buff patch through wear. About 25 per cent have traces of cinnamon across the middle of the breast. No pure white spots on the wing coverts were noted.

TABLE 10

COMPARISON OF OCCURRENCE OF RECTRIX PATTERN IN J. BAIRDI and J. PHAEONOTUS (IN PERCENTAGES)

	Male			Female		
	bairdi	*palliatus*	*J.p.phaeonotus*	*bairdi*	*palliatus*	*J.p.phaeonotus*
Rectrix 4						
Inner web:						
pure black	71	33	83	85	61	80
(otherwise mixed or spotted)						
Outer web:						
pure black	82	95	100	100	97	100
(otherwise spotted)						
Rectrix 5						
Inner web:						
(always mixed)						
⅓ or less black	45	59	10	24	27	8
⅓ or less white	24	7	59	38	23	80
Outer web:						
pure black	26	47	98	15	69	100
nearly all black	18	27	2	31	21	0
mixed	10	26	0	8	10	0
nearly all white	19	0	0	31	0	0
pure white	27	0	0	15	0	0
Rectrix 6						
Inner web:						
pure white	43	16	7	27	14	4
Outer web:						
pure white	89	24	7	88	23	0
(otherwise mixed or with trace of black)						

The same tail-pattern variants are found as in *palliatus;* additionally there are birds with white, and nearly pure white, outer webs of rectrix 5. On rectrix 4 the inner web averages between values for *palliatus* and *phaeonotus,* the outer web being less black than in *palliatus.* The inner web of rectrix 5 averages between values characteristic for the other two species, and the outer is markedly whiter than in *palliatus*. The sixth rectrix is somewhat whiter than that of *palliatus* on the inner web, but on the outer is much whiter. *Bairdi,* then, has a relatively great amount of white on the outer webs of all three feathers, though in total amount, both webs considered, it averages close to *palliatus*. This points to inherent difference in pattern despite similar amount of white. Sexual differentiation is seen chiefly in rectrices 4 and 5 as in *palliatus,* although there is also some in the inner vane of rectrix 6. The sexual dimorphism of the extremely variable outer vane of rectrix 5 takes a peculiar form. Males have more pure white and black variants, females more that are not quite pure black or white. No tendency for more white in males is evident, the dimorphism being a matter of purity; and this is quite different from the condition in *palliatus,* where it is a difference in amount. Again, different controlling factors are indicated.

TABLE 11

MEASUREMENTS OF J. BAIRDI

Measurement	Sex	No. of specimens	Mean with prob. error	Standard deviation	Coeff. of var.
Wing..............	♂	69	70.93 ± .15	1 87	2.63
	♀	32	67.52 ± .18	1.56	2.31
Tail..............	♂	65	66 56 ± .20	2.41	3.62
	♀	28	63 96 ± .29	2.33	3.64
Bill...............	♂	65	8.30 ± .03	.35	4.22
	♀	30	8.18 ± .03	.26	3.17
Bill depth..........	♂	57	6.18 ± .02	.26	4.19
	♀	31	6 03 ± .03	.24	3.98
Tarsus.............	♂	71	20.29 ± .05	.61	3.00
	♀	33	19.99 ± .06	.53	2.66
Middle toe.........	♂	67	11.70 ± .04	.45	3.84
	♀	32	11.62 ± .05	.40	3.44
Hind toe...........	♂	70	8.34 ± .04	.53	6.36
	♀	34	8.12 ± .05	.41	5.04

Variability in wing is slightly less than in *palliatus,* but the tail is as variable as in *alticola.* Instead of fitting into the mainland series of forms in which variabilities of wing and tail increase to the south more or less together (see p. 231), accompanied by lowered correlation, *bairdi* presents decrease in wing, and great increase in tail, variation. It is quite understandable that such an increase in one member only, whether genetic or somatic, would disrupt the correlation. In *bairdi* the coefficient of correlation is only 0.395 ± 0.07. It is not reasonable to suppose that the environment of *bairdi* is so different as to produce such marked differences in variation of wing and tail of a somatic kind. A higher degree of independence of genetic factors for wing and tail seems probable, with relative homozygosity for wing factors. Bill variation and that of the tarsus and hind toe are roughly comparable to those in *J. phaeonotus* and *J. c. dorsalis.* Middle toe variation is less, as in *J. caniceps.*

Although *bairdi* is not large footed like *fulvescens* and *alticola,* it shows a marked correlation of tarsus and middle toe (.476 ± .06), which compares well with that (.534 ± .06) of *alticola*. (This correlation is totally lacking in *J. phaeonotus* and *J. caniceps*.) Tarsus and hind toe are also correlated (.452 ± .06). In *alticola*, both large size and correlation point to a special hereditary mechanism governing these parts. The evidence for *bairdi* points to a similar hereditary linkage, but involving factors for smaller size than in *alticola*, which must have different loci than those producing similar sizes in *J. phaeonotus*.

Bairdi shows a correlation of wing and bill depth at .240 ± .08, which, if reliable, is much greater than in any other forms except *alticola* and *mearnsi*, where it is .434 ± .08 and .427 ± .08, respectively. These correlations and resemblances in pigment weigh in the balance of relationships and make it problematical that affinities of *bairdi* are all with *J. phaeonotus*, although the resemblance still seems closer to that species than to *alticola* and *fulvescens* (see p. 220).

Distribution.—Resident of the Upper Sonoran Zone in the Victoria Mountains of the Cape district of Lower California. The region of the sierra in which it occurs is not more than 50 miles long. So far as known, there are no seasonal movements. Most specimens have been taken above 4000 feet in the section between Miraflores and La Laguna. Brewster's report (1902, p. 147) of a straggler at Triunfo, 1800 feet, is the only exception. The birds remain in winter in the highest part of their range at Laguna Valley, 6000 feet. Apparently there are no winter flocks of any proportion, the birds staying close to the nesting grounds, as is true of all the yellow-eyed forms. The region inhabited is forested predominantly with oak (*Quercus devia*), also with piñon (*Pinus cembroides*) and madroño (*Arbutus penninsularis*), and with cottonwoods (*Populus monticola*) in the canyons. Lamb (MS) took juncos repeatedly in black oak timber at 4000 feet at El Sauce in November and secured some individuals in mesquite bushes and in fan palms. In the spring there is surface water and a good covering of grass in the Laguna Valley.

Bairdi is one of a few juncos that breed under zonal conditions lower than Transition. Its tolerance for the environment in the Victoria Mountains very likely means a special physiological adjustment to it; other juncos usually require a forest of less Austral aspect. This is remindful of certain endemic avifaunas of the Andes, members of which have spread into different (higher) zones in the course of time and apparently have been modified in the process. If the mountains of the Cape once were more Boreal, the juncos may have been gradually forced to their present tolerance in course of gradual climatic change. Either that, or some small pioneering group successfully colonized this atypical habitat. The nature of the region compares most closely, as far as Junco-inhabited regions are concerned, with the Upper Sonoran oak belt of Arizona, which adjoins the habitat of *palliatus* in the Transition Zone and which at times is invaded by that race.

Relationships with other forms.—The nearest point where *J. phaeonotus* occurs is in the Sierra Madre of Mexico across the Gulf of California, roughly 200 miles distant. The isolation of *bairdi* is thus complete. The southern juncos, which are not given to wandering, would not be expected to immigrate to the Cape region today. Yet the connection of the Cape to the mainland of Mexico appears to have been remote geologically, if indeed it occurred at all in Tertiary times. Other members of the fauna do not reflect to any degree a connection in the immediate geologic past. Even if there were a connection when juncolike birds were in existence, it is unlikely that sufficient heights of land existed either north or east to provide continuous habitat. So far as the junco is concerned, the Cape district is now and probably always has been an island. How and when it was colonized must remain unanswered, but that the colonization was earlier than the Pleistocene and was from the south or east I am led to believe from the nature of the birds. The unrelated black-eyed juncos of northern Lower California are now isolated from *bairdi* by 550 miles of intervening desert.

Junco fulvescens

Chiapas Junco

This form is most closely related to *Junco alticola* of Guatemala. It does not interbreed with *alticola,* owing to its isolation. Certain of its characters are such that there is no overlapping, that is, no structural intergradation. Yet the resemblances between these two forms are greater than between *fulvescens* and *phaeonotus,* or *alticola* and *vulcani,* or *fulvescens* and *bairdi.* If its affinities and the degree of differentiation are appreciated, the arbitrary designation of *fulvescens* as race or species is of little moment. I have chosen the latter category in which to place it as more in keeping with treatment of other forms of the genus. *Fulvescens* is barely one step farther advanced in differentiation than a vicarious insular race which shows some overlapping in all characters with its nearest relative. Samples of the species are relatively uniform and the characters do not suggest hybrid origin through an ancient crossing of *phaeonotus* and *alticola.* The form probably has been locally evolved. I fail to see that it is a "variation towards *phaeonotus,*" as stated by Dwight (1918, p. 303). Many of its characters indicate quite the opposite. Its pallor, compared with *alticola,* probably suggested this.

Principal characters of the species.—Iris probably yellowish; mandible yellow; upper mandible dark brown; feet straw color. Back raw umber, wearing to cinnamon brown and Dresden brown. Phaeomelanins of back comparatively yellow, rather than orange, with small amounts of eumalanin mixed throughout the barbules, although more concentrated on the tips. Mixture unlike the condition in northern forms, wherein the two pigments occupy different parts of the barbules. Mass color effect duller and more yellowish or greenish than in *J. phaeonotus.* Back area sharply delimited anteriorly, but confluent with cinnamon brown of inner secondaries and greater secondary coverts and with olive brown of rump. Lores and ocular region black, contrasting with dark olive gray of pileum and of auricular area. Throat and breast pale mouse gray, fairly sharply demarked from dark gray upper parts. Sides near Sayal brown. This color is produced by a scanty deposit of yellow phaeomelanin in the barbules, much more than in *J. p. phaeonotus,* together with eumelanin deposits in the tips of the barbules. Tail with two outer tail feathers part white and a third (number 4) often with a small white spot or tip. Wing and tail short, wings of males averaging 72 mm. Tail short relative to wing, more nearly as in *J. c. caniceps*. Bill very deep and stout, averaging the deepest of any member of the genus. Feet large, tarsus averaging 21.8 mm. in males.

Sexual difference in color is lacking. Nelson (1897, p. 62) describes the females as "rather duller colored." His series, which I have had for examination, is composed chiefly of molting birds, the females being markedly retarded in their molt so that fewer new, brightly colored flank feathers appear. Comparable plumages of the sexes appear exactly alike. Eleven specimens of each sex are all that are available for study and represent most if not all of the known skins of this species. Averages are, therefore, not as dependable as might be desired. Sexual difference in wing and tail averages about 5 per cent. The difference in bill length is about 4 per cent, but there is none in bill depth; tarsus is 1 per cent, and middle toe and hind toe are 3 and 7 per cent, respectively. An immature plumage is not distinguishable.

The effect of seasonal wearing and fading is to lighten the color of the back and make the green and yellow hues more prominent. The bright color of the sides is dulled and reduced in amount by wear. The white of the throat becomes darkened. Changes in the grays of the head are similar to those in *J. phaeonotus*.

Differential characters.—For comparisons with *J. p. phaeonotus* see page 218.

Fulvescens differs from *alticola* most importantly in the color of the sides, which are Sayal brown rather than buffy brown; the breast and underparts are much lighter—pale mouse gray with whitish areas, rather than deep olive gray. The pileum is lighter, not iron gray, and there is more contrast between auricular area and throat. Wing averages 5 per cent shorter; tail, 7 per cent shorter; bill length, 1 to 4 per cent shorter; bill depth, 3 per cent greater; tarsus, middle toe, and hind toe about 6 to 8 per cent shorter. Accordingly, *fulvescens* is smaller to equivalent degree in all measurements except for those of the bill. The bill is shorter but deeper. White is slightly more extensive on rectrix 6 in *fulvescens*.

Nongeographical variation.—Since the species is confined to one group of mountains, no geographically correlated variation is known. The small sample available precludes treatment of individual variation in fashion comparable to that for other forms. No peculiar plumage variations were detected. Tail markings show the following variations: inner vane of fourth rectrix all black (12) or white tipped or spotted (9); outer vane of fourth always black; inner vane of fifth rectrix no more than ⅓ white except for one individual with half the vane white; outer vane of fifth always pure black; inner vane of sixth rectrix ⅔ black (3) or chiefly white (3) but usually ½ to ⅔ white (15); outer vane of sixth pure white (1), pure black (1), chiefly black (4), chiefly white (8), or ½ to ⅔ white (7).

These variants are similar to those found in *J. phaeonotus*, but pure white inner webs of the sixth, and mixed (rather than pure black) outer webs of the fifth rectrix are absent. New types of variants, not found in *phaeonotus*, are pure black outer webs of the sixth, and inner webs of the sixth only ⅓ white. In the dropping out of extreme white variants and the addition of extreme black variants *fulvescens* shows a general reduction of white areas. Also, there are more individuals with greater proportions of black on the characteristically mixed vanes, but there is no decrease in white spotting of the fourth rectrix. The decrease of white is, therefore, not of great magnitude and is more of the order of difference found between the races of *J. phaeonotus.*

TABLE 12

MEASUREMENTS OF J. FULVESCENS

Measurement	Sex	No. of specimens	Mean with extremes
Wing	♂	12	72.56 (68.0–76.6)
	♀	11	67.85 (63.9–70.6)
Tail	♂	9	65.71 (63.0–69.6)
	♀	10	62.92 (57.0–66.0)
Bill	♂	11	8.93 (8.4– 9.5)
	♀	11	8.56 (7.9– 9.2)
Bill depth	♂	9	7.52 (7.2– 7.8)
	♀	10	7.50 (7.2– 8.0)
Tarsus	♂	12	21 83 (20.7–23.3)
	♀	11	21.52 (20.4–22.6)
Middle toe	♂	12	12.63 (12.1–13.0)
	♀	11	12 22 (11.3–13.1)
Hind toe	♂	12	9.41 (8.7–10.2)
	♀	11	8.74 (8.2– 9.3)

As nearly as may be ascertained without the aid of indices of variability, the variations and correlations are roughly comparable to those in adjacent forms, particularly *alticola.*

Distribution.—Limited to the pine forest area of the mountains of interior Chiapas that lie between the Rio Grande, a tributary of the Rio Grijaloa, and the Rio Jutate. The Sierra Madre south of the Rio Grande along the Pacific coast of Chiapas is inhabited by *alticola,* at least at its extreme eastern end.

Particulars relative to plant associations are not known and little information is at hand regarding climate. Nelson and Goldman (1926, p. 577) map the area as pine forest and refer to the rainfall in mountains of Oaxaca, Guerrero, and Chiapas, compared with most other parts of Mexico, as heavy. This impression was gained in part from their field observations of vegetation, some of which must have been made at stations where they took *Junco fulvescens* (San Cristóbal and Teopisca). Nevertheless, it is fairly certain that this area is not subject to the heavy rainfall and humid forest conditions described by Griscom (1932, p. 23) in Huehuetenango of Guatemala, where *alticola* occurs. The uplands of interior Chiapas do not exceed 8000 feet and this must mean more arid conditions than in the high forest habitat of *alticola,* which is chiefly above 8000 feet (Griscom, *op. cit.*, p. 362).

Relationships with adjacent forms.—For *J. phaeonotus* see pages 218 and 226.

J. alticola.—The ranges of *alticola* and *fulvescens* are separated by the lowlands (not in excess of 5000 feet) along the Chiapas-Guatemala border (northern Huehuetenango). The distance between suitable mountain terrains appears to be 40 to 50 miles. There is nothing to suggest any movement across this barrier. Colors characteristic of the two forms show no overlap, and the size characters, though overlapping, show some marked average differences (see p. 227). The two are thus fully isolated and all individuals are constantly and conspicuously differentiated with regard to certain characters.

Junco alticola

Guatemala Junco

This Guatemalan counterpart of *Junco fulvescens* is less restricted in distribution and better known than its relative of Chiapas. Part of its range lies near to that of *fulvescens,* but no evidence of intergradation has been found (see above). There is no intraracial geographic variation.

Principal characters of the species.—Iris variously reported as yellow and orange; lower mandible yellow; upper mandible dark brown; feet yellowish brown. Back raw umber to Prout's brown with pigments arranged in barbules as in back of *fulvescens* (see p. 226). Additional eumelanin seems to account for the slightly darker tone of red-brown. Brown of back sharply demarked anteriorly, but confluent with similarly colored areas on inner secondaries and greater secondary coverts and with olive brown of rump. Lores and ocular region black. Pileum, auricular area, and hind neck iron gray and deep mouse gray. Throat and breast deep olive gray, the chin distinctly lighter. Sides buffy brown, much as in *J. phaeonotus.* Color produced by eumelanins on tips of barbules with very small amounts of phaeomelanin proximally (not in granules). Tail with outer rectrix, and inner vane of next to outer, partly white. Fourth rectrix occasionally spotted. Wing and tail moderately long; wing averages 75 mm. in males. Tail long relative to wing as in *J. phaeonotus.* Bill deep and long. Feet very large, tarsus averaging 23.66 in males.

The plumages of the sexes average the same. Females appear no duller than males on the back and sides and do not possess more rufescent side color, as they do in *J. phaeonotus.* Sexual differentiation in wing and tail is 5 per cent. There are no statistically significant differences in the bill and toes. The tarsus is 2 per cent shorter in females. The sexual dimorphism in size, except for the tarsus, is therefore similar to that in *J. phaeonotus* in being limited to wing and tail. The sexual dimorphism in bill and feet of *fulvescens,* which occupies geographically intermediate territory, cannot be wholly accepted, owing to the impossibility of statistical treatment. Yet with respect to hind toe and bill length it seems certain that there is some true difference. In *alticola,* tail markings show slight sexual dimorphism only (see p. 231).

Seasonal alterations in plumage are comparable to those in *fulvescens.*

Differential characters.—For comparisons with *fulvescens* and *vulcani* see pages 227 and 234–236, respectively.

Nongeographical variation.—Some individuals have distinctly lighter gray breasts than normal, with the gray no darker than olive gray or light olive gray. Although this is a distinct approach toward *fulvescens,* there is never any real confusion of the two in coloration. These light variants are not restricted to the regions adjacent to *fulvescens.* Another variation found in nearly 30 per cent is buff tipping that extends forward from the red-brown of the back onto the hind neck and sometimes the crown. This probably always disappears in late spring. It is not comparable to the reddish crown feathers found in some *J. phaeonotus* and *J. caniceps,* but is like variants of *bairdi.* The pileum and back are variable in color tone to a slight degree. The former may be faintly streaked with a darker tone of gray.

TABLE 13

COMPARISON OF OCCURRENCE OF RECTRIX PATTERN IN J. ALTICOLA AND J. P. PHAEONOTUS (IN PERCENTAGES)

	Male		Female	
	alticola	*J. p. phaeonotus*	*alticola*	*J. p. phaeonotus*
Rectrix 4				
Inner web:				
pure black	80	83	81	80
white spotted or tipped	20	17	19	20
Rectrix 5				
Inner web:				
black with white spot	26	59	44	80
⅔ black	68		56	
½ black	6	31	0	12
⅓ or less black	0	10	0	8
Outer web:				
pure black	96	98	100	100
(otherwise with trace of white)				
Rectrix 6				
Inner web:				
⅓ white	7	0	22	0
½ white	56	93	48	96
⅔ white	37		30	
pure white	0	7	0	4
Outer web:				
black	33	0	41	0
trace of white	31	93	41	100
⅓ white	6		7	
½ white	11		4	
⅔ white	6		4	
with trace of black	11		4	
white	2	7	0	0

Rectrix patterns absent in *J. phaeonotus* are those with less than ⅓ of the inner vane of the sixth white, and those with pure black outer webs of the sixth; these already have appeared in *fulvescens. Alticola* lacks any with ⅓ or less of the inner vane of the fifth black, and any with pure white inner vanes of the sixth, which two types also are lacking in *fulvescens*. *Alticola* and *J. phaeonotus* are essentially identical with respect to the fourth rectrix and the outer web of the fifth. *Fulvescens* differs from *alticola* in the sixth rectrix, where there are only half as many that are black or black with only a trace of white. The greater amount of white spotting (40 per cent) on the fourth rectrix and the lack of an occasional individual with white in the outer web of the fifth are not significant in the sample of *fulvescens*. As to tail pattern, therefore, *alticola* and *fulvescens* are slightly differentiated, less so than the races of *J. phaeonotus* or of *J. caniceps*.

TABLE 14

MEASUREMENTS OF J. ALTICOLA

Measurement	Sex	No. of specimens	Mean with prob. error	Standard deviation	Coeff. of var.
Wing..............	♂	54	75.74 ± .21	2.28	3.01
	♀	30	72.05 ± .29	2.34	3.24
Tail................	♂	50	71.53 ± .23	2.49	3.48
	♀	24	68.08 ± .41	2.98	4.37
Bill................	♂	56	9.00 ± .04	0.48	5.33
	♀	29	8.95 ± .06	0.47	5.25
Bill depth..........	♂	54	7.35 ± .03	0.29	3.95
	♀	28	7.28 ± .05	0.41	5.63
Tarsus.............	♂	60	23.66 ± .07	0.80	3.37
	♀	32	23.11 ± .07	0.63	2.72
Middle toe.........	♂	58	13.34 ± .05	0.51	3.82
	♀	31	13.18 ± .08	0.68	5.14
Hind toe...........	♂	62	9.87 ± .03	0.39	3.94
	♀	32	9.71 ± .05	0.45	4.63

Sexual differences in tail markings are not great. They are confined to rectrices 5 and 6, but chiefly the inner web of the former, much as in *J. phaeonotus phaeonotus*, although to a lesser degree.

It is appropriate here to review certain changes in variability found in passing from *J. caniceps* through *J. phaeonotus* to *J. alticola*. The wing is progressively more variable, the indices in males of *dorsalis, palliatus, J. p. phaeonotus*, and *alticola* increasing as follows: 2.70, 2.87, 2.92, 3.01; females, 1.96, 2.54, 2.93, 3.24. Tail in the same groups increases in variability, though less regularly and to much lesser degree in the males: 3.37, 3.17, 3.36, 3.48; females, 2.77, 3.07, 3.99, 4.37. Associated with this increase is an average diminution in wing and tail length. The tail diminishes less than the wing. Another associated phenomenon is the diminution of coefficients of correlation of the wing and tail. Coefficients for *dorsalis, palliatus, J. p. phaeonotus*, and *alticola* are: .721, .693, .573, .505.

Since in crosses of *caniceps* and *thurberi* correlations were found to be no higher than intraracial correlation (.71), it may be assumed that much of the intraracially correlated variation also is genetic. Two alternate explanations are then possible for the changes in correlation and variation in Central America. These are (1) that increased variability is of a somatic sort, not necessarily manifest to the same degree in wing and tail, and hence the correlated genetic variations of the two are partly obscured; and the alternative explanation (2), that the complex of multiple factors has different members, as it must to account for the general diminution in size, which are not in the same proportion common determiners for wing and tail or which are not linked.

Bill length in *alticola* is distinctly more variable than in *J. phaeonotus* and *J. caniceps.* This sharp increase accompanies increase in average length and the frequency curves are skewed with modes higher than means. Length is comparable to that in *dorsalis,* but in the latter there is no such high variability. Correlation of bill depth with wing length is .434 ± .85. Tarsus and middle toe have a coefficient of .534 ± .063.

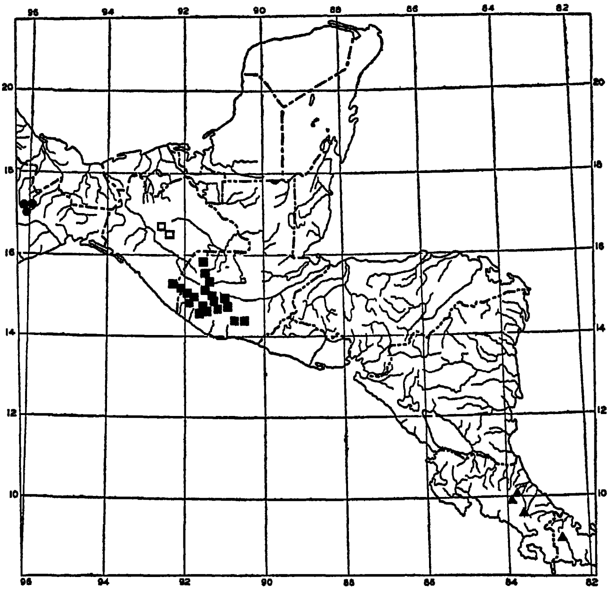

Fig. 8. Distribution of juncos in Central America. Each symbol represents a locality from which specimens have been examined. Dots, *J. p. phaeonotus;* open squares, *J. fulvescens;* solid squares, *J. alticola;* triangles, *J. vulcani.*

Distribution.—Resident of the high mountains of western Guatemala and extreme southeastern Chiapas (possibly also westward in the coastal mountains of Chiapas). Known from localities in the Department of Amatitlán west along the volcanic peaks and altos to southeastern Chiapas, just west of Volcán Tacaná. Also found in the interior in El Quiché and Huehuetenango almost to the Chiapas border. The birds inhabit the Boreal Zone (Griscom, p. 362, p. 65) in pine, mixed pine and oak, and humid cypress (*Cheirostemon*) and spruce forests usually above 8000 feet and most commonly at higher elevations up to 11,100 feet. Some localities, if they represent the actual point of capture, are as low as 6500 feet. Although Griscom compares the lower levels where *alticola* occurs to the southern Rocky Mountains of the United States, a majority of the population would appear to exist at elevations where the forest is very humid, with epiphytes abundant and sometimes with dense undergrowth. It is this upper humid forest that probably is lacking or restricted in the range of *fulvescens.*

Relationships with adjacent forms.—For *J. fulvescens,* see page 229.

J. vulcani.—This species, so different from other juncos that its generic assignment has at times been questioned, of course has no close relationship with *alticola.* It is separated geographically by 500 miles of country uninhabited by juncos. Although the highlands of Salvador and Honduras would seem to provide some limited areas of suitable habitat, no juncos have been discovered there, and there is no possibility of their occurrence in Nicaragua.

Junco vulcani

Irazú Junco

This terminal member of the series of Central American forms is the most aberrant species of the genus. Its distinctness has aroused suspicion concerning its generic affinities. Ridgway (1901, p. 272) comments as follows: ". . . even including *J. vulcani,* which is far out of place in any other recognized genus, *Junco* is a much more homogeneous group than *Spizella,* or indeed than most recognized genera containing an equal number of species." In some outstanding particulars such as the stripes on the back, the absence of pure white in the tail, and the prominently ridged culmen, *vulcani* is distinctly different. All these features are to some degree suggested in the rest of the genus. Not to be overlooked are the considerable resemblances to *alticola* in plumage coloration, exclusive of the stripes, as also in the color of the iris. Dimensions of *vulcani* are either similar to *alticola* or represent extremes of trends in differentiation that are in evidence in *phaeonotus, fulvescens,* and *alticola.* Too great emphasis should be avoided with respect to presence or absence of stripes in genera of the Emberizinae. Examination of details of feet, wing, and bill shows a reasonably close similarity in types. As genera of sparrows are now defined, I believe, in accordance with Ridgway, that *vulcani* definitely falls closest to *Junco.* Nothing would appear to benefit from designating a subgenus for it exclusively.

The question of including other groups of Central American or South American sparrows in the genus *Junco* has been studied only casually, as it is incidental to the main objectives of this investigation. *Phrygilus* of the Andean region, especially *P. alaudinus,* is as suggestive of *Junco* with respect to coloration as any Neotropical group known to me. However, the different type of tail markings in *alaudinus,* which consist of spots rather than stripes or longitudinal areas, is perhaps a greater departure from *Junco* than the obsolete white of *vulcani.* The bluish slate coloration of the head is not closely similar to that of *Junco.* The back is striped.

The characters of plumage, feet, and bill which are used throughout the sparrows to define genera are often unconvincing. It would be highly desirable to compare carefully the internal structure of *vulcani* with that of the other *Juncos,* as well as to compare related genera. It is not impossible that strong evidence might be disclosed which would not uphold the present allocation of *vulcani.* Other factors which would have some weight, in my judgment, are similarities in habit and, in a rough way, in habitat. The correspondence of *vulcani* with other juncos is fairly good in these respects, though more knowledge of details is desirable. The species is more terrestrial than are other juncos.

Principal characters of the species.—Iris variously reported as yellow, golden, or orange; mandible, maxilla and feet flesh color, resembling those of northern juncos. Bill exceptionally straight in outline on all sides, the width proportionately less than in other juncos; culmen distinctly ridged, the basal third with two grooves on either side parallel to ridge; relatively little inflation of maxilla. Back dark citrine, olive citrine, or buffy citrine, each feather with a large, somewhat guttate stripe of black on distal part of vane. Stripes fairly sharply limited anteriorly, becoming very faint, and dark citrine, variable in amount, confined to feather tips. Line of demarcation corresponds to margin of brightly colored area of other juncos. Back coloration and pattern extends with little modification to wing coverts and secondaries. Rump area sharply delimited, without stripes. Head smoke gray to light grayish olive, with olive citrine tipping. Lores and ocular region black as in *alticola.* Underparts light grayish olive, becoming lighter on belly and more tinged with olive buff. Sides buffy olive. Underparts generally similar to *alticola* except for more prevalent olive and yellowish hues of gray. Wings and tail blackish, with considerable edging of buffy citrine.

The citrine of the back is produced by eumelanin and a yellow phaeomelanin that has no trace of orange when viewed microscopically, the pigment being purer yellow than in *alticola* and *fulvescens.* The eumelanin is distributed in the barbules as in these species, that is, it is not confined to the tips of the barbules. The pigments of the flank feathers are comparable to those of the flanks of *alticola,* but the phaeomelanin is pure yellow and the eumelanin of the barbule tips is more extensive although well delimited. The phaeomelanin is nongranular.

Wing and tail moderately long, although possibly relatively short compared with body size. Wing of males averages 78 mm. Tail relatively long, less than 5 per cent shorter than wing. Bill deep and long. Feet extremely large, tarsus averaging 26.9 mm. in males.

Sexual dimorphism in plumage is absent. Wing and tail average 5 per cent shorter in females. No differences in bill or feet associated with sex can be proved statistically except for tarsus, which is 2 per cent shorter in females. The pattern of dimorphism is thus the same as that of *alticola.*

Wear decidedly alters the appearance of the head through the reduction of the olive or citrine overcast on the dorsal surface. Wear never completely removes this color, but it always accentuates the demarcation of head and back. The faint striping of the head is more obvious in worn plumage. The light-colored margins of rectrices and remiges disappear, especially the buff tips on the outer rectrices.

Nongeographical variation.—The newly grown outer rectrix probably always has a buff tip 1 to 2 mm. wide on the inner vane. Sometimes this is almost white, but often it is dark so as to contrast weakly with the remainder of the feather. Also on the inner vane of this rectrix the pigment may be pale distally to form blotched or clouded areas. This strongly suggests a blotching seen in other species of juncos on rectrices that are adjacent to white-bearing rectrices or that have white spots elsewhere on the vane of the same feather. The variation in color of the pileum, already noted, has a great range. Comparison of birds from different mountain summits reveals no colonial differentiation.

TABLE 15.

MEASUREMENTS OF J. VULCANI

Measurement	Sex	No. of specimens	Mean with prob. error	Standard deviation	Coeff. of var.
Wing..............	♂	26	78.17 ± .24	1.84	2.36
	♀	18	74.10 ± .27	1.76	2.37
Tail..............	♂	23	74.43 ± .43	3.06	4.11
	♀	17	70.70 ± .47	2.85	4 03
Bill length.........	♂	27	9.32 ± .06	0.44	4.68
	♀	18	9.53 ± .07	0.44	4 58
Bill depth..........	♂	19	7.21 ± .04	0.25	3.48
	♀	14	7.18 ± .07	0.39	5.50
Tarsus.............	♂	23	26.96 ± .09	0.68	2.54
	♀	19	26.23 ± .12	0.79	3.00
Middle toe.........	♂	23	14.66 ± .07	0.49	3.35
	♀	19	14.27 ± .07	0.47	3.32
Hind toe...........	♂	24	10.86 ± .10	0.79	7.26
	♀	19	10.76 ± .07	0.48	4.47

Variability in wing is materially decreased, being lower than in males of *dorsalis*. Thus, the southward increase in variability in the yellow-eyed juncos of the mainland does not hold for this species. Tail, on the other hand, is exceedingly variable, the most variable in the genus. As in *bairdi,* the coefficient of correlation of wing and tail is not especially high (.496 ± .108) where wing and tail each varies to a different degree. The correlation is not appreciably lower than in *alticola,* however.

Bill length does not vary so greatly as in *alticola,* but is comparable to that in *J. phaeonotus.* The frequency curve is skewed as in *alticola.* Bill depth is similar to that in *alticola.* Correlation between wing, tail, bill length, and depth is general in this species, whereas such relations involving the bill are found in only a few other juncos. The following are the coefficients: wing and bill length, .494 ± .104; wing and bill depth, .319 ± .129; tail and bill length, .354 ± .123; bill and bill depth, .599 ± .092. Tail and bill depth were not at all correlated. Unfortunately, the high probable errors detract from the significance of these coefficients. Those above .4 must certainly have some true value. The common factors that govern wing and tail would also seem to influence bill dimensions or to be linked to factors that do so. The lower correlation of tail with bill length and its absence in the case of tail and bill depth may be due to the unusually high variation in the tail, which either is controlled by independent factors connected solely with the tail or is somatic.

The only correlation involving the foot is that of tarsus and bill depth at .349 ± .129. There is no correlation of middle toe with tarsus such as in *alticola,* where the correlation suggested common or linked factors for long tarsus and long middle toe.

Distribution.—Resident of the highest peaks of central and southern Costa Rica, and of Volcán Chiriquí in extreme western Panama. The volcanoes of Irazú and Turrialba in the central cordillera are inhabited, as are also the highest peaks of the Dota Mountains and the paramo of Chirripo in the cordillera of Talamanca. It probably occurs at other points along this cordillera south to Chiriquí.

The juncos inhabit the scrub growth above timberline, never coming below 8500 feet. Austin Smith states in correspondence that they enter "to some extent the upper edge of the (oak) forest, but they are mostly found above timber line to the very crest, 11,400 ft. [of Irazú]. On . . . Turrialba, it is not common—not more than 25 individuals. . . . On the paramo [of Chirripo] above 11,000 ft., there are only 3 species of birds commonly met with," the junco being one of them. "*Junco vulcani* nests during April; mostly in tufts of grass; but sometimes in low bushes. It is essentially a terrestrial species; . . . owing to more cover on the northern volcanoes it is there more skulking. . . . This species as well as the one peculiar to Guatemala obtain a goodly part of their food supply from the seeds of various herbaceous Salvias. If my memory be not at fault its nuptial chant much resembles" that of the Arizona junco. The habitat of *vulcani* evidently is bleak and cold, but detailed comparison with the climate of the highlands of Guatemala cannot be made.

Comparison of vulcani and alticola.—The obvious differentiation of these two forms requires no special treatment for practical purposes of identification. There remain for detailed consideration comparative aspects that may bear on the problem of interrelationships. Throughout the genus the variation in tail white follows certain restricted lines. There is always a progressive diminution in white in the rectrices toward the center of the tail. No matter in what species, the rectrices, whether second, third, fourth, or fifth, that adjoin more lateral rectrices with appreciable amounts of white, display some variation in the form of white spots, or of diagonal or longitudinal areas of white, either terminally or separated from the tip. The major axes of such areas never lie across the feather, although in some forms they tend more that way than in others. In *vulcani,* the buff (occasionally whitish) tips sometimes reach fair proportions and, as they are placed diagonally along the margin of the inner web, are extremely similar to white tips and spots that appear on rectrices 4 and 5 in *alticola.* In *alticola* in such feathers that are predominately black the outer web rarely has white. The tail of *vulcani* is, then, quite conceivably merely an end type in the same series of variations found in other juncos. It is as though the last white or partly white tail feather were lost, leaving its faintly marked neighbor. The clouded effect on the outer rectrix, already mentioned, is contributory evidence.

The stripes of *vulcani* have no special counterpart in *alticola,* but in various members of the genus, in which there is eumelanin in the back area, occasionally there are weak, but quite apparent, dorsal streaks. In these the center of each feather vane is distinctly more blackish than the margins. Of course, the striped juvenal plumage in all young juncos is also suggestive, but this condition, although almost certainly primitive, is so prevalent in all sparrows as to have no particular significance here. Young of *vulcani* are heavily striped, with extension of the stripes to the head, rump, and underparts. The colors of juvenal *vulcani* and *alticola* are closely similar throughout.

Dr. M. Sassi of Vienna reports in correspondence that the iris of juveniles of *vulcani* is greenish yellow and that the bill and feet are like those of adults. The young he reports upon were taken on the 18th and 19th of July, 1930, and may have been acquiring adult coloration of the soft parts. The yellow eyes and flesh-colored bill of adults are a peculiar combination. The eyes agree well with the condition in other southern juncos, but the bill is like northern forms and possibly has been independently evolved. The characteristic bill shape of *vulcani* is not foreshadowed in *alticola.* Ratio of depth to length is more like that in *dorsalis,* and the shape of the bill is much closer to that in juncos with less inflated bills than to *alticola* and *fulvescens.* Also, in juncos with less inflated bills there are faint grooves paralleling the ridge of the culmen, but these never reach the development found in *vulcani.*

The wing of *vulcani* is 3 per cent longer than that of *alticola;* the tail, 4 per cent. Bill is 3 per cent longer, and because of its different proportions its depth is 1 per cent less. Tarsus is 14 per cent longer, middle toe and hind toe 10 per cent longer. The foot, then throughout is large, without great alterations in proportion. Such an increase in foot size is not without parallel, for the tarsus of *alticola* is 10 per cent longer than that of *phaeonotus.* The proportions of *vulcani* are continuations of trends recognizable in *fulvescens* and *alticola* and the differences are in keeping with the degree of spatial separation and isolation of *vulcani.*

The pigments of *vulcani* are like those of *alticola* in the following respects: mixture of phaeomelanin and eumelanin of the back throughout each barbule, separation of these pigments in the flank feathers into separate parts of the barbules, and lack of granulation of phaeomelanin in the flank feathers. The phaeomelanins of the juncos south of *phaeonotus* are more nearly pure yellow and produce more olive and yellowish hues of brown than in *phaeonotus* and *caniceps. Vulcani* carries this to an extreme. The tones of grays are similar, though more mixed with faint yellow in *vulcani.* Facial mask, demarcation anteriorly of back area, and confluency of back color with that of the wings are characteristics of markings that *vulcani* shares with *alticola* and other southern juncos.

These facts all contribute to the view that *vulcani* is a member of the series of Central American juncos which, beside showing the extremes of certain trends, preserves some juvenal and probably ancient characteristics that may be like those of the prototype of the genus. Undeniably it has characters peculiarly its own, evolved probably in the course of its long isolation. Bill characteristics and tail coloration may fall in this category.

Rassenkreis **Junco oreganus**
Oregon Junco

This rassenkreis, the most extensive one in the genus in number of races, is composed of forms between which there is interbreeding or, at least, structural intergradation. Some of them are strongly differentiated, as for example *mearnsi* and *townsendi*, whereas others are faintly or very incompletely differentiated. *J. o. oreganus, shufeldti, montanus, mearnsi, thurberi, pinosus, pontilis,* and *townsendi* are included. In the breeding season the group occupies suitable areas on the Pacific coast from Yakutat Bay, Alaska, to the San Pedro Mártir Mountains, Lower California. In the north it is limited to the coast, but it extends farther inland in the Rocky Mountains of Montana and Wyoming, there culminating in *mearnsi,* which is found in many mountain ranges well within the Missouri River drainage. South of Oregon, Idaho, and northern Wyoming this *oreganus* type of junco is restricted to regions west of the Great Basin. Migrations vary from a complete type in the northern division of *montanus* to a state of absence in *pinosus* and *townsendi.*

Principal characters of the group.—In so extensive a rassenkreis few characters peculiar to the group remain constant throughout. The most important character is the presence, in the sides, of phaeomelanin which is sharply complementary to the black or gray of the hood. The phaeomelanin of the sides is granulated in the barbules, unlike that of the yellow-eyed juncos, which is uniformly distributed. The hood is convex posteriorly and is dark, although it may be as light as, or lighter than, that in *hyemalis.* Some phaeomelanin always is present in the middorsal area; eumelanin rarely is absent there. The two pigments are not mixed in the barbules, as in *fulvescens* and *alticola,* but occur in separate segments of the barbules. The mass effect produced by them is similar, although it is usually a redder, less greenish, hue of brown. Iris some hue of brown; bill flesh-colored; size moderately large to small.

Junco oreganus mearnsi

Racial characters.—*Mearnsi* may be distinguished from *montanus* by the following characters: slightly broader areas of phaeomelanin on sides, of pinkish cinnamon hue (not equal to any of Ridgway's colors) instead of vinaceous fawn, fawn color, or army brown; granular phaeomelanin of sides orange-yellow instead of yellow, and eumelanin absent from tips of barbules. Head neutral gray or slightly darker instead of dark neutral gray to black (males), or deep to dark neutral gray (females). Back usually less blackish, but phaeomelanin component often similar. Average measurements of *mearnsi* are greater than those of southern populations of *montanus:* wing, 3 per cent; tail, 5 per cent; bill depth, 3 per cent. White often more abundant on rectrices 3, 4, and 5. Sexual dimorphism in color less.

The major features that differentiate *mearnsi* from *J. caniceps* are essentially those of the entire *oreganus* group. Presence of phaeomelanin in the sides and absence of gray eumelanin, with the resultant hood marking, distinguish *mearnsi.* The back of *mearnsi* has a less abundant, yellower phaeomelanin and there is eumelanin in the tips of the barbules; the latter pigment is absent in *caniceps*. The brown area of the back is confluent with the brown and buff of the wing coverts and inner secondaries, instead of being sharply limited as is the reddish brown of *caniceps*. The head is a darker neutral gray (see p. 201). The lores and ocular area are less prominently black.

Wing and tail averages differ no more than 1 per cent in *mearnsi* and *caniceps*. These differences are not certainly reliable statistically. *Mearnsi* tends to be the smaller, particularly with regard to tail. The females of the two forms are more similar than the males in the samples at hand (see pp. 182, 241). Bill length of males is the same as in the shorter-billed populations of *caniceps*, but the females average 2 to 3 per cent shorter. Bill depth is 1 to 5 per cent less in both sexes of *mearnsi*, depending on the population of *caniceps* which is used for comparison. Bill depth approaches values for the Colorado and Utah populations of *caniceps*, but bill length is similar to that of the Colorado and Nevada groups. Thus it appears that size differences are all very small, many scarcely significant except that the trend in *mearnsi* in each difference is toward values characteristic of the main group of races of *J. oreganus*.

The white of the tail of *mearnsi*, so often reported to be great in amount, is remarkably similar to that of the Nevada populations of *caniceps* (see p. 240). *Mearnsi* does exceed the Nevada birds in amount of white on the third rectrix; 17 per cent of males and 5 of females have white on this feather, whereas such variants do not appear in *caniceps*. *Mearnsi*, nevertheless, is less differentiated from Nevada *caniceps* than the latter is from the other populations of *caniceps*. This still does not argue for a great degree of distinctness of the Nevada group, nor for special affinity with *mearnsi*, but merely emphasizes the incomplete differentiation of *mearnsi* with respect to tail pattern.

For comparisons with *aikeni* and *hyemalis* see pages 346 and 314–315, respectively.

Nongeographical variation.—Mearnsi is an especially variable race with regard to color, particularly when compared with *Junco caniceps*. This variability is seen in breeding areas remote from points of contact with *montanus* or *caniceps*. The range of variation in head color is fully as large as that represented in extremes of *caniceps* from Utah and Nevada. The pigment of the sides is variable in intensity, and sometimes is but slightly different from the vinaceous hue of *montanus*. Backs are uniform with respect to the eumelanin component, but some are much more ruddy, owing to phaeomelanins, than are others. The result is that certain individuals resemble the less blackish variants of *montanus*, being snuff brown, whereas others are drab so that the back is indistinctly contrasted with rump and wings and even with the head when buff tippings are present on the nape.

Reddish color on the pileum, a not uncommon variation in *caniceps*, was found in only one of 600 individuals. Reddish back feathers on birds from regions remote from points of *caniceps* contact were found in only three individuals (Montana and northern Wyoming). Whether these are new mutants, or whether they are the result of mixture with some stray *caniceps*, is not certain. In this connection should be recalled the significant occurrence

TABLE 16

OCCURRENCE OF RECTRIX PATTERN IN J. C. MEARNSI AND J. C. CANICEPS (IN PERCENTAGES)

	Male			Female		
	mearnsi	*J. c. caniceps* (Nevada)	*J. c. caniceps* (Colorado)	*mearnsi*	*J. c. caniceps* (Nevada)	*J. c. caniceps* (Colorado)
Rectrix 2						
trace of white	1	0	0	0	0	0
Rectrix 3						
Inner web:						
trace of white	17	0	0	5	0	0
Outer web:						
trace of white	7	0	0	0	0	0
Rectrix 4						
Inner web:						
pure black	1	0	7	12	6	10
trace of white	18	100	93	40	94	90
mixed	64			47		
trace of black	12			0		
pure white	4	0	0	0	0	0
Outer web:						
pure black	25	40	57	62	69	61
trace of white	21	58	41	15	31	39
mixed	22			22		
trace of black	21			0		
pure white	11	2	2	0	0	0
Rectrix 5						
Inner web:						
mixed	4	10	47	5	47	76
trace of black	26			52		
pure white	70	90	53	43	53	24
Outer web:						
mixed	14	38	70	32	66	67
trace of black	22			27		
pure white	64	62	30	41	34	33
Rectrix 6						
Inner web:						
pure white	100	100	100	98	100	90
Outer web:						
pure white	100	96	85	100	94	90

at the time of the spring migration, May 5, 1919, of a fully characterized *J. c. caniceps* at Glendive, Montana, far north of the range of the species.

White on the wings is somewhat more prevalent (1.82 per cent) than in *caniceps* (1.29 per cent), but it shows no greater incidence in regions nearest the range of the white-winged junco, *J. aikeni.* In addition to individuals with distinct white spots, there are many in which the coverts are edged with light gray. A single individual with a whitish throat patch has been noted.

Continuity of the areas of phaeomelanin across the breast is a frequent variation found in 8.10 per cent of all *mearnsi.* Its occurrence is much higher in females, 11.6 per cent, compared with males, 3.6 per cent. This difference exists in spite of small sexual difference in the hood pigment and no difference in the hue of the phaeomelanin. When a cross connection is present, it may extend irregularly across the margin of the hood, or it may form a line anterior to the margin, thus leaving a gray stripe posterior to it. It seems usually to represent a replacement of the gray hood pigment. This variant is comparable to that found in 25 per cent of the unrelated species *bairdi,* where the sides are likewise richly supplied with phaeomelanin. In *mearnsi* the phaeomelanin is granulated; in *bairdi* it is not.

TABLE 17

MEASUREMENTS OF J. O. MEARNSI

Measurement	Sex	No. of specimens	Mean with prob. error	Standard deviation	Coeff. of var.
Wing..............	♂	74	81.22 ± .17	2.22	2 73
	♀	46	77.16 ± .19	1.91	2.47
Tail...............	♂	73	73.15 ± .20	2.55	3 48
	♀	45	69.51 ± .23	2.30	3.30
Bill length.........	♂	64	8.22 ± .03	0.36	4.37
	♀	43	8.00 ± .04	0.38	4.75
Bill depth..........	♂	54	6.17 ± .02	0 25	4.05
	♀	38	6.05 ± .03	0.24	3.96
Tarsus.............	♂	74	20.14 ± .04	0.55	2.73
	♀	44	19.75 ± .05	0.52	2.63
Middle toe	♂	62	11.52 ± .04	0.42	3.64
	♀	44	11.30 ± .05	0.47	4.15
Hind toe...........	♂	66	8.04 ± .03	0.36	4.47
	♀	44	7.99 ± .04	0.38	4.75

Sexual dimorphism in color is restricted to the head, where the difference in gray is comparable to that in *caniceps.* An overcasting of buff on the hood is more frequent in females, but it is always limited to the extreme feather tips, so that the hood is demarked dorsally to some degree and is never obliterated as in some retarded plumages of *J. hyemalis.* Males may have buff tips on the hind neck. Probably such overcasting is more prevalent in first-year birds of both sexes, but accurately aged material taken in the fall is lacking and so this cannot be determined. Ages and sexes are less distinctly differentiated than in some other races of *J. oreganus,* though in all races the differentiation is less complete than is commonly supposed.

Wear alters the head but slightly. The back does not brighten with abrasion, even though the terminally situated eumelanin of the barbules is partly lost. Much of the phaeomelanin of the back feathers is situated in the more distal parts of the vanes, so that its loss probably compensates for the diminution of the dark tips of barbules. The color of the sides becomes less pinkish, more yellowish or cinnamon, as the season advances. The effect is comparable to the brightening of the phaeomelanin of the back of *caniceps.*

No intraracial geographic variation in the tail pattern of *mearnsi* can be found that grades either toward *J. aikeni,* with its greater amount of white, or toward *caniceps,* with less white. For discussion of resemblance to Nevada *caniceps* see page 239. Sexual dimorphism occurs chiefly in rectrices 3, 4, and 5.

Coefficients of variability for wing and tail are slightly greater than in *J. c. caniceps;* those for other measurements are similar. These differences are not at all comparable to those between *J. caniceps* and the species of Mexican and Central American juncos. The coefficient of correlation of wing and tail is .865 ± .02, distinctly higher than in *caniceps* and much higher than in still more southern groups, where coefficients of variability are large Tarsus and toes are not correlated. Wing and bill depth are definitely correlated, with a coefficient of .427 ± .07. This peculiar relation, absent in *J. caniceps, J. phaeonotus,* and *J. o. montanus,* is all the more unexpected because there are no prominent differences in averages of these characters compared with adjacent forms. Certainly there must be a different arrangement of factors than in *J. caniceps,* where the coefficient (*dorsalis*) is 074 ± .07. Sexual dimorphism is about 5 per cent in wing and tail, and 2 per cent in bill and feet, as in *J. caniceps.*

Geographical variation within the race.—Although no geographical variations can be clearly demonstrated at this time, it is not impossible that they may exist. The breeding material has not been representative of a variety of localities. Smaller size may occur in Montana north of the Yellowstone, but the sample is inadequate, and large size is again encountered in Saskatchewan. This possible diminution is unrelated to intergradation with *montanus* in western Montana. The birds of the Big Horn Mountains, Wyoming, are especially large. Populations of *mearnsi* are not isolated to the degree found in *J. caniceps,* except possibly in the region north of the Missouri River and in the Big Horn Mountains. The beginning of geographic variation in the direction of *montanus* is dealt with later (pp. 244–245).

Distribution in breeding season.—Populations of *mearnsi,* apart from those in which there is interbreeding with other forms, are found principally in the mountainous regions centering about the Yellowstone Plateau and Teton Range. Outlying populations, somewhat isolated from this fairly continuous inhabitable region, extend the breeding limits of the form into Saskatchewan, eastern Alberta, eastern Idaho, and north-central Wyoming (Big Horn Mountains). The form is to be thought of as one essentially endemic to that segment of the Rocky Mountains which lies north of the southern Wyoming deserts and east of the upper Salmon River of Idaho and the upper Missouri and Jefferson rivers of Montana. This mountainous section is moderately arid compared with northern Idaho and parts of interior British Columbia. Lodgepole pine (*Pinus contorta*) dominates the lower coniferous forests and there is junco habitat in aspen forests (*Populus tremuloides*). At higher altitudes Englemann spruce (*Picea englemanni*) forests predominate. *Mearnsi* apparently does not encounter the extreme aridity experienced by *caniceps* over great sections of its range, although it may tolerate relatively dry, scrubby growths of aspen locally and inhabit scanty yellow pine and Douglas fir forests on certain prairie ranges (see Saunders, 1921, p. 13). Nothing comparable to the *Cercocarpus* habitat of *caniceps* is occupied. Owing to the lower elevations of the Boreal areas, juncos may breed at altitudes as low as 5000 feet in parts of Montana and Idaho. The lower limits in central Wyoming are often 7000 feet.

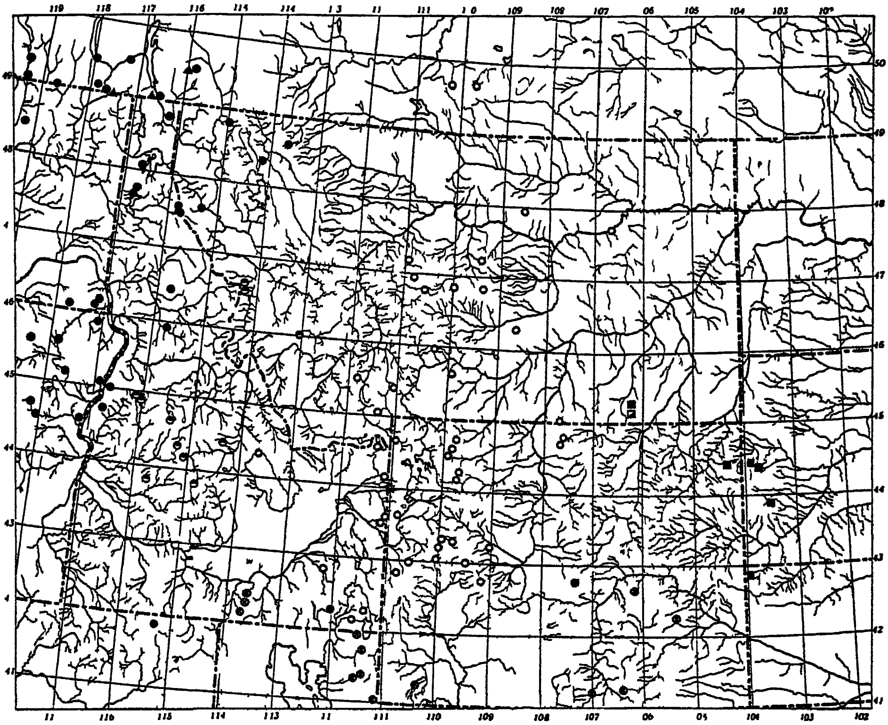

Fig. 9. Distribution of *Junco oreganus mearnsi* and neighboring forms in the breeding season. Northern Rocky Mountains of United States (Idaho, Montana and Wyoming, and parts of eastern Oregon and Washington, southern Canada, western South Dakota and Nebraska, and northern Nevada and Utah). Each symbol represents a locality from which specimens have been examined. Circles, *J. o. mearnsi*; dots, *J. o. montanus*; half dots, intermediates between *J. o. mearnsi* and *J. o. montanus*; circles enclosing crosses, hybrids of *J. c. caniceps* and *J. o. mearnsi*; triangles, hybrids of *J. o. montanus* and *J. hyemalis*; solid squares, *J. aikeni*; partly solid square, hybrids of *J. aikeni* and *J. o. mearnsi*.

Wyoming.—In Boreal Zone (Cary, 1917) in mountains of northeastern section from Salt River and Wind River ranges of Lincoln and Fremont counties northward and in Big Horn Mountains (see appendix for intermediates of central Wyoming).

Montana.—Chiefly in Boreal Zone in mountains west of about longitude 107° and south and east of the Missouri, Jefferson, and Beaverhead rivers. There is some evidence that populations just west of the last-named river represent the beginning of intergradation with *montanus*. Known definitely from Crazy, Little Belt, Big Belt, Big Snowy, and Big Horn mountains, from the mountains of extreme southern Musselshell County, and from those adjoining Yellowstone Park. Also occurs north of Missouri River in Little Rocky Mountains, Phillips County, and along Missouri River in Garfield County; probably also in other similar ranges in this section of the plains where there are limited areas of Transition Zone.

Saskatchewan.—Cypress Hills, in southwestern corner of province.

Alberta.—Known from Eagle Butte on southeastern border, adjacent to the Cypress Hills of Saskatchewan.

Idaho.—In eastern section of state north of Bear Lake, populations of pure *mearnsi* occur, but west of the lower Bear River and south of the Snake River all populations appear to be mixed. North of the Snake River on the Montana border pure populations are found west as far as the Lemhi Mountains. Westward in the Sawtooth and Salmon River mountains there is intergradation.

Distribution in winter.—*Mearnsi* winters commonly in the lower mountains of Arizona, New Mexico, and Colorado, the largest representations of winter birds coming from southeastern Arizona and the eastern flank of the mountains of Colorado. It is also known in winter from points on the plains as far east as central Nebraska, western Kansas, and the panhandle of Oklahoma. It occurs in western Texas (Presidio County), and in Chihuahua (south-central) and Sonora (northern). It migrates south through Utah and Nevada in small numbers; wintering records seem to be lacking for Nevada and are scarce for Utah (Presnall, 1935, p. 209). However, an intermediate between *mearnsi* and *montanus* is at hand from Belleview, Blaine County, Idaho, taken January 7, 1936. Of four record specimens for California, three are from the Colorado River region in Imperial County and one from western San Diego County. Apparently all birds leave the breeding grounds even though they remain in the fall until October or, sometimes, early November. Compared with *J. c. caniceps*, *mearnsi* leaves the breeding range more completely in winter and spreads out on the plains in greater number. The extreme limits of record are similar in the two forms; they are commonly associated in flocks in winter in Colorado and in the oak belt of New Mexico and Arizona.

Relationships with adjacent forms.—For *J. c. caniceps*, *J. h. hyemalis*, and *J. aikeni*, see pages 200, 326, and 351, respectively.

J. o. montanus.—The breeding Oregon juncos east of the Cascade and coast-range mountains from central Oregon to central British Columbia display considerable regional differentiation as well as much individual variation. Although all birds in this area may be considered to belong to a single race, *montanus* (formerly known as *shufeldti* or *couesi*; see Appendix), it is not possible to indicate any one phase of plumage out of the heterogeneous mixture as typical, nor is there a single center of racial differentiation. There are two main divisions of the group which are only very incompletely differentiated. The southern division occupies northern and western Idaho, eastern Oregon, and adjacent parts of Washington and Montana. It is fairly stable over this area and cannot be considered merely a hybrid or intergrade between the more northern division of *montanus* and *mearnsi*. It is essentially the same in such widely separated areas as Crook County, central Oregon, and Boundary County, extreme northern Idaho. It is only this division of *montanus* with which *mearnsi* interbreeds.

Study of the interrelations with *montanus* rests largely on series of breeding males taken by me at localities in Idaho beginning at the western border and extending east to the southeastern section of the Sawtooth Mountains at Alturas Lake. Juncos were secured at five localities spaced 20 to 25 miles apart. Those on the west were from normal populations of southern *montanus;* those at Alturas Lake were not all pure *mearnsi,* but the intergradation at that point had progressed more than halfway toward *mearnsi.* The principal points of contrast between *montanus* and *mearnsi* are those of coloration of the head, back, and sides. Size and tail pattern differ but slightly.

Head color effects the most complete differentiation of the two forms. In analyzing intensity of head color, ten successive stages were distinguished, ranging from a dark black (type 1), rare even in northern *montanus,* to the palest type of *mearnsi.* The ventral surface of the head was used chiefly. Southern *montanus* usually are of types 5, 6, and 7, with occasional darker individuals, the average being about 6. Pure populations of *mearnsi* are made up of types 9 and 10, the average falling about halfway between them. The graph (fig. 10) shows individual variation and change geographically in head color. The groups are spaced at intervals scaled to the actual spatial separation in an air line west to east. In males the uniformity across Oregon is evident. About 35 miles east of the Snake River the variability increases, significantly in the paler categories, and the average quickly drops. East of Alturas Lake the curve is projected on the basis of a small number of typical *mearnsi* from the region of the Lemhi Mountains, Idaho. A level doubtless is attained about here which is equal to that found in the Yellowstone region and which persists throughout the remainder of the range of *mearnsi.* Breeding range is more or less continuous across this entire area, certainly so in the region of intergradation in which I collected.

The females, similarly classified, form a more irregular curve, no doubt owing to the greater chances of variation from sampling. Several points of significance appear, however. Sexual dimorphism is twice as great in *montanus* as in *mearnsi.* The break of the curve at the region of intergradation is less abrupt. But also the curve shows that *montanus* influence first appears phenotypically at a point farther west than in males; similarly, typical *montanus* averages appear farther west.

Because back color is a complex of phaeomelanin and eumelanin mixed to produce a brown, the analysis of back variants is not easy. When the black component becomes especially large it may invade the basal portions of the vanes to produce solid blackish areas, whereupon the brown regions become more restricted distally. This redistribution, which is independent of tone of brown, is fairly certainly an effect of intermixture of *J. hyemalis.* The eumelanin component was classified as follows: *aa* and *a,* eumelanin of back extensive and intense, but usually not darkening the brown areas which may be distinctly bright (type *aa* is attributable to *hyemalis* without doubt); *b,* average extension of blackish areas and moderate component of eumelanin in brown areas; *c,* distinctly smaller black component in brown areas that results in lighter tones. The phaeomelanin component of the brown parts is classed with respect to intensity and, to some degree, amount: 1, clear reddish yellow; 2, less distinct yellow, the combination appearing duller brown; 3, dull yellow, with eumelanin producing a very dull gray-brown. *Mearnsi* all fall in classes 2*c* and 3*c*. *Montanus* of the southern area are of classes 2*c*, 3*c*, and 3*b*,

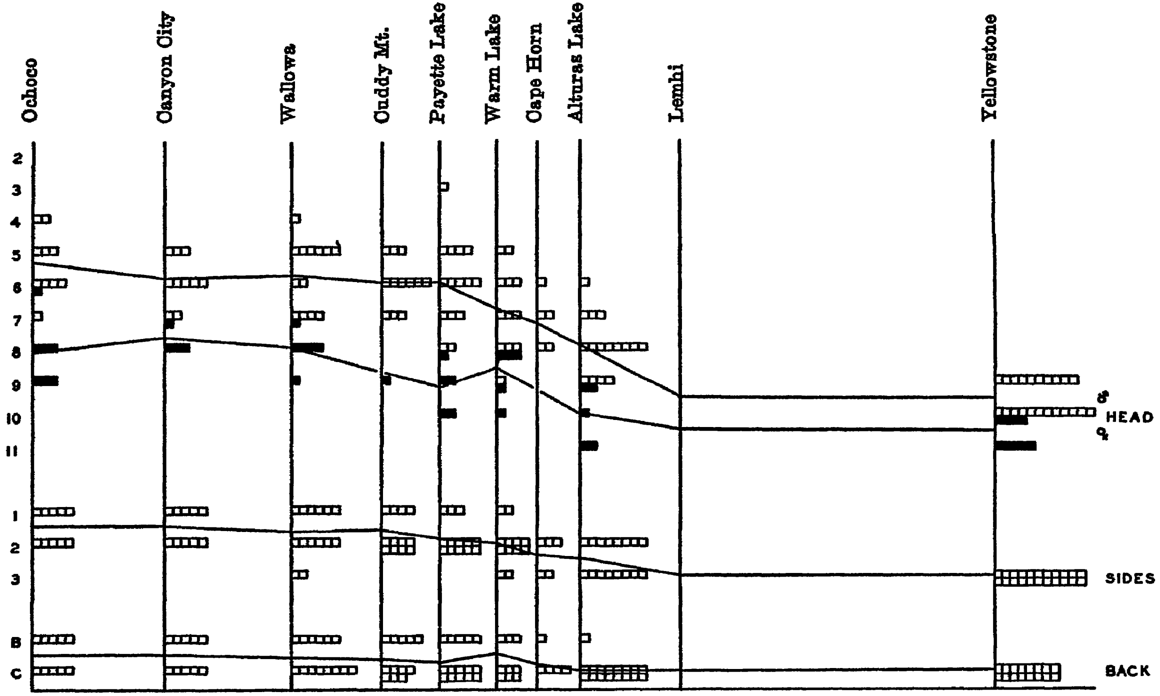

Fig. 10. Occurrence of head, back, and side variants in a series of samples from the range of *J. o. montanus* (southern) east through that of *J. o. mearnsi*. Samples spaced to scale geographically. Lines connect averages for groups. Open squares, individual males; solid squares, females. For explanation of variants see pages 245, 247, and 248.

with infrequent occurrences of 2*b*, and rarely others. The chief point to be noted in the transitional area is the disappearance of type *b* as *mearnsi* is approached (see fig. 10). The principal change takes place in the interval between Warm Lake and Alturas Lake, and so is restricted to a narrower zone than is that of the head. The change in the back is purely a shift of average, not an intergradation of completely different types as with the head.

The following list is a synopsis of symbols used in designating stages in reduction of intensity of pigments in the *oreganus* and *hyemalis* artenkreise. The symbols at the top of each column represent extreme saturation. Some members of the series of back types are not completely equivalent quantitatively, as explained in the text where new symbols are introduced.

BACK		HEAD
PHAEOMELANIN	EUMELANIN	
ooo	*aaa*	1
oo	*aa*	2
o or *p*	*a*	3
t	*b*	4
1	*c*	5
2	*d*	6
3	*dd*	7
4	*y*	8
5		9
6		10

The backs of females are distinctly poorer in blackish pigment than those of males, so that the phaeomelanins are more prominent and the general tone is lighter. All fall into class *c* in the southern part of *montanus* and in *mearnsi*. Phaeomelanin is either of type 2 or 3, rarely 1 in *montanus*. There is, therefore, no differentiation of the races on the basis of intensity of eumelanin as in the males.

This situation in the females and the fact that the differentiation in males is associated in general with head color, the latter more prominent and more sexually dimorphic in *montanus*, suggest some degree of correlation of head and back. That this is not perfect is obvious from the fact that distinctly dark-headed females of *montanus* are still of class *c*, as are the gray-headed *mearnsi*. Possibly it takes an extreme development of black, as in the heads of the darker males of *montanus*, to bring any concomitant extension or intensification of the eumelanin component in the back. To test this hypothesis, correlations of head type with back in male individuals of northern and southern *montanus* and in *montanus–mearnsi* intermediates have been determined. The general correlation for all groups combined was .427 ± .038. It appeared possible that this correlation might be due in part to the diverse natures of the geographically different populations used in the correlation table. For example, if a population of pure *mearnsi* and one of *montanus* were combined, a high coefficient of correlation would result, indicative of the association of the characters in the races, but it would not necessarily be based on a fixed association in individuals. Consequently, separate correlation coefficients were determined for northern *montanus,* southern *montanus,* and the intermediates. The coefficients were: northern *montanus,* .402 ± .076; southern *montanus,* .435 ± .054; *montanus–mearnsi* intergrades (Warm Lake to Alturas Lake), .504 ± .086.

Inspection of all the correlation tables shows that types *a* and *b* are limited for the most part to birds with heads that are type 6 or darker. Only 8 per cent of type *b* are of head types pales than 6, as compared with 41 per cent of *c* that are paler than 6. In comparable fashion the pale back, *c,* occurs almost entirely with head types 5 or lighter. Only 5 per cent of *c*'s constitute exceptions, while 35 per cent of *b*'s are of head types darker than 5. Clearly there is some interdependency of eumelanins in these areas.

Any effect of head color on the back is seemingly suppressed in females. But, this may be because in southern *montanus* and in *mearnsi,* females rarely attain head color darker than 8 and never darker than 6, types which even in males are almost entirely associated with back *c.* There may, then, be no sex-limited situation, for certain dark-headed females of northern *montanus* attain back *b.* Probably there is some interaction of factors for back and head so that when a critical point in dark-headedness is reached the back cannot normally remain uninfluenced, and contrarily, when the head is extremely pale no great intensity of pigment in the back is possible.

A significant fact to be deduced from the coefficients is that intraracial correlation is not appreciably lower than in interracial hybrids. The racial characters and the intraracial variants are all part of the same complex. The intermediate populations are thoroughly intermixed, and extreme types that appear are probably chiefly Mendelian segregates. Variation is higher at a point like Warm Lake because of the contribution originally of parentage of diverse types from either side.

Side color is not completely differentiated in *montanus* and *mearnsi,* although it is much more so than is back color. Three categories were recognized: 1, extreme *montanus* type with colored areas moderate in extent and with nearly all feathers brownish or vinaceous fawn owing to small amounts of eumelanin additional to the dull pinkish phaeomelanin; 2, some feathers of the area brownish, but also some with conspicuous yellowish or cinnamon and no eumelanin; 3, all feathers yellowish or pinkish cinnamon, the area extending medially onto the breast farther than in types 1 and 2. All three types are found in *montanus,* but 3 is rare. *Mearnsi* are all of type 3, or they may show an even greater medial extension of the color (see p. 240). Type 3 might properly be subdivided into a yellowish type and a pinkish cinnamon one, both occurring regularly in *mearnsi,* but the latter solely in this race. However, wear and fading make it impractical to attempt such a distinction among worn plumages. Some difficulty is encountered in evaluating the width of the colored area because of variation in the make of skins.

The graph (fig. 10) indicates the intergradation and occurrence of types in *montanus* and *mearnsi.* Although it might appear that there is some definite change toward *mearnsi* in the Wallowa area, this actually is not the fact. The

Wallowa group is quite normal for *montanus* in proportions of types; the groups farther west happen to be lacking in type 3. Type 3 occurs occasionally north through Idaho to the northern limits of *montanus* in central British Columbia. The principal intergradation coincides with that of head color rather closely.

The sides of females are similar to those of males and intergrade in the same way. Type 3 is almost lacking west of Payette Lake and type 1 is lacking east of Warm Lake. The only sexual differences consist in slightly less dark brown on the lower flanks in type 1 and a somewhat paler yellow on the average in type 2. In *mearnsi* the yellowish type of 3 is a little more prevalent than the pinkish cinnamon type. Side color is not correlated individually or geographically with the phaeomelanin of the back or with eumelanin of back and head. Phaeomelanin increases in the sides toward *mearnsi,* whereas that of the back becomes reduced.

The wings of southern *montanus* and *mearnsi* differ on an average by only 2 per cent. Populations of *mearnsi,* as in the southern part of Montana adjoining the Yellowstone region, may measure 1 per cent less than *mearnsi* as a whole. The birds from Wyoming adjacent to Idaho are, however, not smaller. With such minor and rather unreliable differences in averages locally, it is almost impossible to indicate the region of intergradation with *montanus,* even though the general averages of the races are significantly different. As far east as Alturas Lake there is no sign of increase in wing length. Tail length, which differs by 5 per cent in southern *montanus* and *mearnsi,* shows no increase eastward until Alturas Lake is reached, where it rises definitely to an intermediate point, 3 per cent lower than in *mearnsi.*

The white of the third rectrix, which occurs irregularly in *mearnsi,* is about the only point of difference in the tail pattern that may be dealt with in the intergrades. Such variants appear in the Wallowa Mountains, but not with regularity except east of Payette Lake. The proportion of occurrence at Alturas Lake is fully as high as in *mearnsi.*

The situation north of the extensive intergradational belt in Idaho is not known in any detail. Saunders (1921, p. 128) reports breeding *mearnsi* from Jefferson, Silver Bow, Deer Lodge, and southern Powell counties. Apparently no critical examination of specimens was made, although the populations must have been essentially of *mearnsi* type. An early May bird from Deer Lodge County, which I have examined and which was taken after the migration dates given for the area, is somewhat atypical of *mearnsi.* Saunders tentatively gives the dividing line between *mearnsi* and *montanus* as the Northern Pacific Railroad between Helena and Missoula; thus, it is an east–west boundary line. From evidence at hand from scattered breeding birds, the Idaho intergrades, and from the knowledge of the northward extension of *mearnsi* in central Montana, I think that the belt of intergradation must extend more nearly north and south. From the Sawtooth Mountains, Idaho, it runs northeast through the southern Bitterroot Valley and northern Powell and Lewis and Clark counties. Two birds from Idaho City, Boise County, Idaho, suggest a population of a degree of intermediacy about equal to that at

Warm Lake. A series from the west side of the northern Bitterroot Valley, near Missoula, is *montanus* with only two individuals that suggest the beginning of intergradation. The series is about like that from Payette Lake, Idaho.

The populations of northwestern Montana, including that of the type locality of *montanus,* are in no way different from those of southern *montanus* in northern Idaho and eastern Oregon. Their considerable variability is encompassed in the normal range of variation found elsewhere in the race. The head colors of males are all of types 5, 6, and 7, average 5.8, and although the sides in some individuals look like *mearnsi,* such types are no more frequent than in Oregon and Idaho.

The meeting of *mearnsi* and *montanus* occurs in a region where there are no barriers to distribution. At least in Idaho and in parts of Montana they meet in areas of nearly continuous forest habitat. There is more discontinuity within the range of *mearnsi* in northeastern Idaho than in the region of principal intergradation. That there is some change in forest condition that reaches a critical point in the area of intergradation, it is difficult to conceive. In the range of *mearnsi* the forests are more open and arid than in parts of the range of *montanus.* Yet there is much diversity within the area of each race. *Mearnsi* frequently occupies arid lodgepole pine forest, but in parts of the Fraser River Valley *montanus* thrives under comparable forest conditions. If *montanus* were restricted to the humid forests of northern Idaho and British Columbia, one would be tempted to assume that such an environment was essential to this race and not to *mearnsi.* Adaptive value of the brightly colored sides of *mearnsi* or of its dull head is quite unlikely. The race appears to me to be possessed of characters of long standing which are not related to present climatic and vegetational conditions. In the zone of junction with *montanus* there is increased variability such as would arise through interbreeding of two diverse stocks. If the intermediates had differentiated *in situ* as the result of intermediate conditions, I believe the chances are that they would not show the same degree of variability, but only variability equivalent to that of either extreme population. If it were clear that the intermediates had to cope with two different phases of environment, corresponding to those of the racial extremes, highly variable intermediates might evolve, but in the absence of any indication that characters are associated with a particular environment this seems unlikely.

To speculate further, it is not probable that extreme types could have arisen and have become segregated into separate areas, as have *montanus* and *mearnsi,* if those areas were always in contact. One form surely would have swamped the other unless there was some distinct advantage in the new variant, for example, of the *montanus* sort. Isolation for a long period doubtless made possible the present differentiation, while at the same time ability to interbreed was not impaired. The present intergradation is to be viewed as a secondary junction similar to the interbreeding of *caniceps* and *mearnsi* and *caniceps* and *J. o. thurberi,* but not at all like the intergradation of *J. p. phaeonotus* and *palliatus.*

Most of the characters which separate *mearnsi* and *montanus* show blending, and multiple factor inheritance is the probable mechanism. Side color tends to segregate into two or three categories, but the separation is not perfect and there is some degree of blending. No evidence of dominance is at hand. It is to be noted that the chief differentiating characters of *mearnsi* and *montanus,* namely, the colors of head, back, and sides, involve the same pigments in both races. Proportions of phaeomelanins and eumelanins, with some modification of the hue of the former, alone account for the differences, great as they may appear to the eye. This was not true with *mearnsi* and *caniceps,* where the total absence of certain pigments was responsible for differences in back and sides. Thus, although in both these pairs of forms there is interbreeding, the differentiation of *caniceps* and *mearnsi* seems more fundamental, irrespective of modes of inheritance. Isolation of breeding ranges also is more complete in the case of *mearnsi* and *caniceps.*

Junco oreganus montanus

In areas north and west of the range of *Junco o. mearnsi,* the black-headed juncos vary with respect to color to a degree unparalleled in the forms of the southern Rocky Mountains. In addition, the birds of California, Oregon, Washington, Idaho, and British Columbia show geographic differentiations, some of which are fairly sharply outlined both as to characters and range, and others of which are so incomplete as to make impractical a categorical separation into races. Within this mosaic of geographic variation, exclusive of the extremes in central and Lower California and central coastal British Columbia, it is doubtful if true racial units exist; instead, there are many independent geographic gradients in characters that run in different directions through the area. One can recognize some poorly defined breaks in the gradients that permit the mapping out of races that combine certain average values for various characters, but these races are in a sense artificial. This state of affairs should be fully appreciated by anyone attempting to identify birds pertaining to these regions.

The juncos of eastern Oregon, eastern Washington, interior southern British Columbia, northern and western Montana, and northwestern Idaho comprise a group which may be treated as a race. Within this race two divisions exist, a northern and a southern one. The extreme variants in each of the divisions are so different as to suggest well-defined races. But although these variants may be characteristic of an area, they are so frequently found elsewhere, or they are of such erratic occurrence, that they fail to differentiate the geographic divisions to a satisfactory degree. This composite race has had various names applied to it. It must now, by rule, bear the name *montanus* (see Appendix A).

Montanus as represented by the type series is not clearly an intergradient or hybridized group as supposed by Dwight and as I at one time thought. The critical fact not heretofore emphasized is that the race formerly known as *shufeldti* or as *couesi* is variable, enough so to include the original *montanus* series (see p. 392). The southern section of *montanus* as here considered is, then, like Ridgway's *montanus*. The type, unfortunately, is a light-headed variant, an extreme for the race.

Racial characters.—Compared with that of *J. o. oreganus,* the back of *montanus,* although quite variable, is grayer or less reddish; it never is Prout's brown, Brussels brown, or raw umber as in *J. o. oreganus.* This character effects a nearly perfect separation of the races outside of intermediate areas. Other characters that incompletely differentiate the two are lighter head color in *montanus,* averaging 4 to 6 (see p. 247) instead of 3.2 as in *J. o. oreganus,* and less rufescent, and often less dusky, sides. Wing and tail average 5 per cent longer; tarsus and toes 3 to 5 per cent shorter. The amount of white usually is greater on rectrices 4 and 5 (for details, see pp. 253 and 272).

For characters which differentiate *montanus* from *J. hyemalis* and from *J. o. shufeldti* see pages 314 and 264, respectively.

Nongeographic variation.—Color of head, back, and tail, and many of the measurements, are dealt with in a later section on geographic variation. For discussion of variation in side color see page 248. The variation in the side found in northern *montanus* is the same as that in southern *montanus.*

Reddish pileum, a mutation occasionally met with in *J. caniceps, J. phaeonotus,* and once in *J. o. mearnsi,* is unknown in *montanus.* However, brownish overcast of the head, which in extent may be very great, is extremely common. This rarely involves bases of the feathers to the extent that the red mutation does. It is a feature probably latent in all juncos of this and similar races, but it is most pronounced in this group; it finds expression in young and in females most often. Brownish overcast is, however, no certain indication of age or sex, but is properly viewed as a retarded phase of plumage (Mayr, 1933, p. 2), sometimes omitted entirely, but in other individuals found even after the first year. It is not highly correlated with the intensity of the black of the head. Undue concern with this feature may lead to confusion of the more significant characters of the race.

White on the wing coverts occurs in 1.17 per cent of the 342 breeding *montanus* that were examined. Odd color patterns in the ventral part of the hood and occasionally on the pileum are not uncommon. They appear to be due to incomplete molts with retention of some feathers of a previous retarded plumage. This is seen most frequently in the paler types of females and occasionally suggests the variants in *mearnsi* in which phaeomelanin is mixed along the ventral margin of the hood.

In parts of the range of the race adjacent to *J. hyemalis,* yet not in the regions where interbreeding occurs at all extensively, birds with some *hyemalis* characters appear as rare variants in otherwise typical populations of *montanus.* These so evidently have to do with the problem of hybridization with *hyemalis* that discussion of them will be deferred to a later section.

Sexual dimorphism of head color is about twice as great as in *mearnsi* (see fig. 10). Associated with this, the sides and back are often slightly lighter in females because of the lesser eumelanin component (p. 247). Sexual dimorphism occurs in rectrices 3, 4, and 5 about as in *mearnsi.*

The sides, and particularly the back, tend to brighten in the course of the year, becoming yellowish in those variants which have relatively large amounts of phaeomelanin. In the duller individuals seasonal change is not pronounced and is comparable to that in *mearnsi.*

TABLE 18

OCCURRENCE OF RECTRIX PATTERN IN J. O. SHUFELDTI, J. O. MONTANUS AND J. O. MEARNSI (IN PERCENTAGES)

	Male				Female	
	shufeldti	*montanus N.*	*montanus S.*	*mearnsi*	*montanus S.*	*mearnsi*
Rectrix 3						
Inner web:						
trace of white	0	0	1	17	0	5
Outer web:						
trace of white	0	0	1	7	0	0
Rectrix 4						
Inner web:						
pure black	17	23	4	1	20	12
trace of white	44	60	50	18	61	40
mixed	40	15	46	64	20	47
trace of black	0	2	1	12	0	0
pure white	0	0	0	4	0	0
Outer web:						
pure black	62	65	46	25	78	62
trace of white	15	8	16	21	9	15
mixed	19	22	19	22	11	22
trace of black	2	5	17	21	2	0
pure white	2	2	3	11	0	0
Rectrix 5						
Inner web:						
mixed	10	9	5	4	30	5
trace of black	42	32	30	26	52	52
pure white	48	58	65	70	17	43
Outer web:						
mixed	17	23	9	14	13	32
trace of black	17	26	25	22	52	27
pure white	67	51	66	64	33	41
Rectrix 6						
Inner web:						
pure white	100	100	100	100	95	98
Outer web:						
pure white	100	100	100	100	100	100

Geographic variations within the race.—*Montanus* is almost lacking in variants with white on the third rectrix and in those with pure white inner webs of the fourth rectrix. Otherwise the same variants are present as in *mearnsi.* The average amount of white on the fourth and fifth rectrices is less in *montanus.* In this respect the southern population stands about halfway between *mearnsi* and the northern group; the average for the fourth rectrix is closer to the northern, that for the fifth rectrix nearer *mearnsi.* Thus the interracial differentiation is no greater than intraracial differentiation with respect to these highly variable features.

Individual variability indicated by the coefficients is comparable to that in *mearnsi.* The coefficient of correlation for wing and tail is .646 ± .033 for males, .520 ± .069 for females; this is lower than in *mearnsi,* which has the highest correlation of any form of junco. The significance of wing and tail correlation is subject to the criticism that the correspondence may be due in part or entirely to a general variation in size which might affect all dimensions of the animal. F. B. Sumner has suggested the need of determining whether there is a special correlation of these parts additional to general variability in size. He was able to do this in *Peromyscus* by determining the partial or net correlation, eliminating size. Unfortunately, in birds there is not available a good measurement of general size comparable to the measurement of total length in mammals. Even though new collections were to be made in which total length was ascertained at time of preparation, the extreme flexibility of the bird's neck would in some degree complicate the measurement. The best substitute that can be offered for total length is weight.

TABLE 19

MEASUREMENTS OF J. O. MONTANUS, SOUTHERN DIVISION

Measurement	Sex	No. of specimens	Mean with prob. error	Standard deviation	Coeff. of var.
Wing..............	♂	141	79.25 ± .12	2.06	2.61
	♀	51	74.52 ± .15	1.58	2.14
Tail..............	♂	141	70.00 ± .13	2.28	3.28
	♀	51	65.69 ± .20	2.15	3.29
Bill length.........	♂	125	8.25 ± .02	0.33	4.03
	♀	55	8.00 ± .03	0.28	3.57
Bill depth..........	♂	125	5.99 ± .02	0.25	4.23
	♀	52	5.93 ± .03	0.28	4.67
Tarsus.............	♂	150	19.93 ± .03	0.53	2.67
	♀	58	19.96 ± .05	0.58	2.94
Middle toe.........	♂	150	11.38 ± .02	0.39	3.42
	♀	59	11.21 ± .04	0.42	3.74
Hind toe...........	♂	150	8.02 ± .02	0.41	5.11
	♀	60	7.87 ± .03	0.35	4.39

One hundred breeding male birds from within the range of southern *montanus* have been weighed (average 17.7 gr.). Wing and weight were found to be correlated to so low a degree (.237 ± .063) as to be of doubtful significance. This, together with the fact that tarsus and wing are not correlated, indicates the absence of any great correspondence between length of appendages and body size. In other words, there are no general size fluctuations which affect all parts; otherwise, variation in the tarsus and wing would correlate. To show more adequately that there is a net correlation over and above size, I have calculated the partial correlation (Fisher, 1934, p. 174) of wing and tail, eliminating weight. The coefficient is .623.

Despite the numerous factors which affect the weights of birds (see Linsdale, 1928, p. 312), the moderate variability of this measurement, compared with that of mammals, makes it fairly reliable. The breeding male juncos used in these calculations were taken over a period of six weeks. Practically all of them were devoid of obvious deposits of fat and rarely were their stomachs empty. The coefficient of variability was 5.2 per cent, which is about twice that of wing length but equal to that of some of the toe and bill measurements.

The unusual correlation of wing and bill depth found in *mearnsi* is lacking in *montanus*. Tarsus and hind toe show a low correlation of .356 ± .048.

Measurements of the northern division of *montanus* that occupies the Cariboo and interior Skeena districts of British Columbia show some minor differences compared with those of the southern group. Wing length is only 1 per cent shorter and tail is almost identical, so that no significant differentiations in these respects exist. Bill length and depth are 3 per cent less; tarsus is only 2 per cent longer, but the difference is significant statistically. Bill depth carries farther the trend toward small size seen in passing from *mearnsi* to southern *montanus*. Bill length, on the other hand, is the same in *mearnsi* and southern *montanus*. The degrees of difference in measurement between the divisions of *montanus* and between southern *montanus* and *mearnsi* are therefore comparable, though differing in detail. All differences are so purely matters of average as to be of no utility in attempts to segregate individuals into race groups.

Sexual dimorphism of wing and tail increases to 6 per cent compared with 5 in *J. caniceps* and *J. o. mearnsi*. Since tail is 12 per cent shorter than wing, compared with 10 per cent in *mearnsi*, an additional stage in tail shortening is manifest. Sexual dimorphism of bill and feet is almost lacking, except in bill length.

Head color varies geographically as well as individually. Normally, males of a population in the southern area are chiefly of categories 5, 6, and 7 (see p. 247), those of the northern area 3, 4, and 5. The average, as shown in figure 11, changes between the United States boundary and the southern Cariboo District (Clearwater River) of British Columbia. Just how abrupt this change is cannot be stated without more evidence from samples from the intermediate Kootenay District, but the rapid change in a twenty-mile interval between Meadow Creek and Creston suggests that most of the change may take place within sixty miles of the border. Increased variation at this point is well shown in the graph. The differentiation of the northern and southern groups on the basis of head is 69 per cent, but when it is considered that there is a certain amount of error in assignment to categories, identification of only about 60 per cent would be possible.

Back color, the components of which have already been fully analyzed in the racial hybrids, shows some average change northward through the Kootenay area. The phaeomelanin component continues to increase northward to the Skeena River. The graph which represents separately the alteration in average in the two pigments indicates that the principal change in the eumelanin occurs slightly south of the points where alteration in head pigment and phaeo-

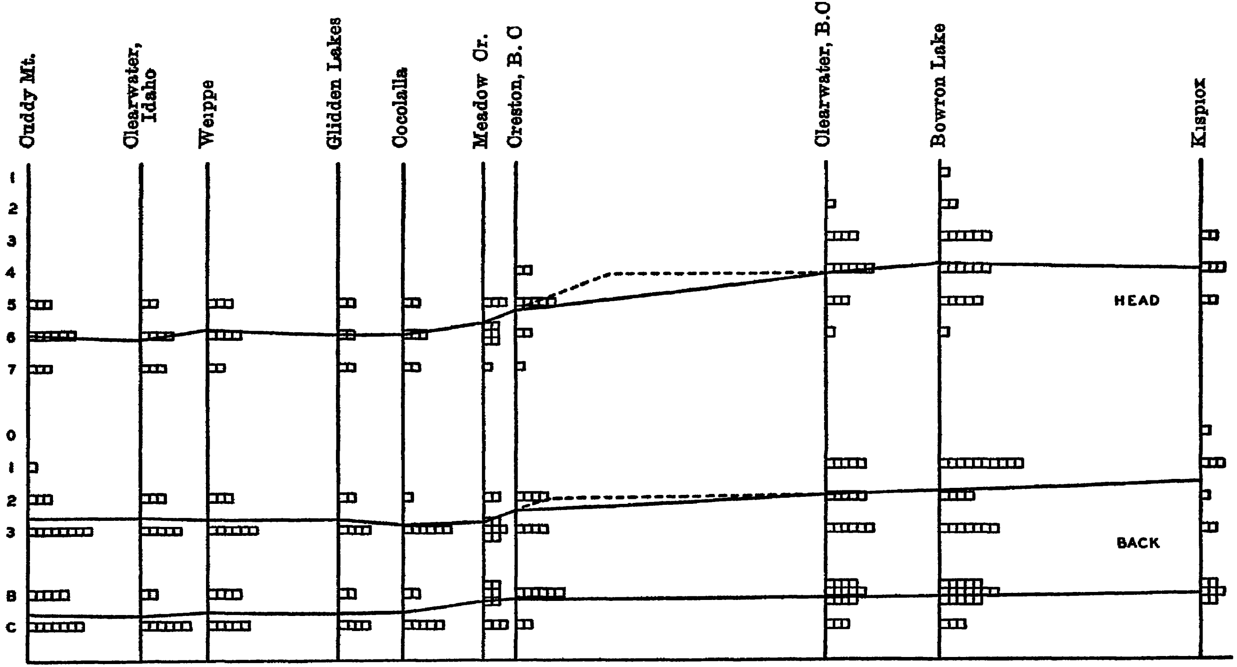

Fig. 11. Occurrence of head and back variants in males in a series of samples of *J. o. montanus* ranging from central western Idaho north and northeast to central interior British Columbia. Samples spaced to scale geographically. Lines connect averages for groups. Broken line represents probable curve projected on basis of differences in Meadow Creek and Creston groups. Two components of back coloration shown. For explanation of variants see pages 245 and 247.

melanin of the back is most pronounced. This situation exists despite the fact that in individual variation head and eumelanin of the back are correlated to a moderate degree (see p. 247). However, there is enough lack of conformity of head and back and enough variation in samples of the size dealt with to account for the imperfect geographical correlation of the changes.

Summary of intraracial geographic variation.—The incompletely differentiated northern and southern divisions of the race merge in the southern Kootenay area, where there is continuous forest habitat. Head color changes abruptly between Meadow Creek, Idaho, and Creston, B. C., as does the average for phaeomelanin of the back. The latter continues to change northward as far as the Skeena River. Eumelanin of the back changes principally south of the Canadian border. The average dimensions of bill and tarsus differ in the two geographic extremes, but the region of intergradation could not be localized on the basis of material at hand. The geographic intergradation of these various characters, because of their partial independence, does not appear to result from junction of types that once were more diverse, but may be an instance of differentiation *in situ* in which each character is affected independently.

Distribution in breeding season.—Populations of *montanus* occur in the mountains of Oregon east of the Cascades and north of the low desert areas of the southeast; in western Idaho north of the Snake River; in northwestern Montana; in eastern Washington; and in British Columbia north through the interior, west of the Selkirk Range and, more northerly, west of the continental divide and east of the coast ranges to the valley of the Skeena. It is especially difficult to define accurately the breeding range along its eastern limits in British Columbia because of the nature of the intermixture of *montanus* with *hyemalis*. Occasional stray *hyemalis*-like individuals may nest far west of the continental divide, as in the Skeena Valley and at Barkerville, but they are rare. Not until the continental divide is reached, as at Yellowhead Pass and Banff, is the mixture great. Even eastward of this point many *montanus*-like hybrids appear (for full discussion of zone of mixture see pp. 328 ff.), and some are known from points as far north as the interior of Alaska.

This breeding range is extremely diverse in character. In places the forest habitat is relatively arid, and is dominated by lodgepole pine (*Pinus contorta*) as in the range of *mearnsi;* but elsewhere, as in parts of northern Idaho, the habitat is remindful of coastal humid forests with rich growths of epiphytes and mosses and is dominated by hemlock (*Tsuga heterophylla*) and cedar (*Thuja plicata*). On the whole, the range does not include extensive forest habitats like those of the humid coastal archipelago of British Columbia or of the Puget Sound region. In Oregon there are large tracts of western larch (*Larix occidentalis*) and yellow pine (*Pinus ponderosa*) which, especially the latter, provide open parklike areas especially favored by juncos. Conditions here are similar to those within the range of *thurberi* in the Sierra Nevada. In parts of British Columbia, black spruce (*Picea mariana*) and timber-line associations are common habitats, as are also the hemlock and lodgepole pine forests. Probably if any environmental factor is correlated with the characteristics of these inland birds, it is not a particular forest habitat, but a general prevalence of fairly dry conditions. Certainly the tolerance of this junco for varied local environments is high.

British Columbia.—Occurs in the forested areas of the interior from elevations below 1000 feet in the north to timber line. It is not known north of the Skeena drainage basin or east of it in the Peace River Valley, except as hybrids. The race extends west to the headwaters of the coastal rivers in the coast range, where some intergradation becomes apparent. Southeasterly, relatively pure populations are restricted to areas west of the Selkirk Range and the Cariboo Range. The distribution is irregular and interrupted by Upper Sonoran areas in the Yale district, but is continuous in the Kootenay region southward into Idaho, eastern Washington, and northeastern Montana.

Washington.—Known from the mountains of eastern Okanagan County and above 3000 feet in the Blue Mountains of the southeast. Also occurs, beyond doubt, in the mountains of Ferry, Stevens, and Pend Oreille counties north of the Columbia and Spokane rivers.

Idaho.—Occurs in timbered areas over most of the northern part of the state south through Idaho, Adams, and Washington counties. Populations from western Valley County are but slightly intergradient. Lower limits of occurrence are at 1800 feet in the Clearwater River Valley and in more arid mountains, such as on Cuddy Mountain, at 4000 feet.

Montana.—Breeds in suitable forest areas northeast of the vicinity of Missoula and west of the continental divide, except locally as at Saint Mary's Lake.

Oregon.—Occupies the mountains east of the Cascades; these are chiefly the Blue and Wallowa mountains, which form an almost continuously habitable belt from Crook County eastward to Wallowa County south of the plains of the Columbia and north of the deserts of Malheur and Harney counties.

Distribution in winter.—Winters commonly in the lower mountains of Colorado, New Mexico, and Arizona. Also occurs generally in California, but more abundantly toward the east, where it is the predominant wintering form in suitable places in the desert areas. Rarely reaches the northwest coast of California. Extends southward to Chihuahua, and in Lower California to latitude 32° and possibly farther, though there are no definite records. There are records for Texas east to 97° longitude (Gainesville) and southeast to the vicinity of San Antonio (Ingram, Kerr County) and Fort Clark (Kinney County). In Oklahoma, Kansas, and Nebraska occasional individuals may appear, especially in the western regions, but also as far east as Lawrence, Kansas. Birds may remain as far north as southern British Columbia, in the Okanagan and lower Fraser valleys. Also winters in eastern Washington and Oregon, and Idaho, Nevada, and Utah. Occasional strays, which I have been able to verify by examination, have been taken far to the eastward, as for example at Waukegan, Illinois, and Branchport, New York. A well-characterized male has been examined that was taken November 29, 1936, near Monclova, Lucas County, Ohio. It is not unlikely, then, that *montanus* does actually occur in other states east of the Mississippi River, where it has been reported. Some of the record specimens have in the past been misidentified, however, and sight records are not to be relied upon.

Montanus and *shufeldti* on their wintering grounds cannot be identified with more than 80 per cent accuracy. Birds with 3*b* or 3*c* type of back may be identified as *montanus*, for these back types are found in 50 per cent of *montanus* but in only 4 per cent of *shufeldti*. Size criteria must be relied on largely in dealing with birds of back types 1 and 2. Back type *o*, or extreme ruddy individuals of type 1, may safely be considered *shufeldti*. Unfortunately, in the earlier stages of my work when great numbers of wintering *shufeldti* and *montanus* were examined, color criteria were thought to be adequate for these races and size was not considered; reëxamination and measurement of these specimens is not now feasible. At the present writing, juncos of back type 3 must be relied upon to a considerable degree to outline the range of *montanus* in winter. However, in the eastern limits of the winter range of Oregon juncos, the presumption, unless there is good evidence to the contrary, is that the birds are *montanus* and are not those from the breeding range of *shufeldti*, which as now known is restricted to coastal areas. Nevertheless, true *shufeldti* does occur in small numbers with *montanus* in the Great Basin and southern Rocky Mountains, where indeed the type was taken. It is regrettable, therefore, that certain wintering birds earlier identified cannot at present be considered as critically determined. The winter range of *montanus* outlined above rests on unquestionable specimens of this race.

Some direct evidence for the migration and wintering range of birds of the Cariboo district is afforded by a banding return provided me by Mr. T. T. McCabe. A breeding bird which was banded at Indianpoint Lake, near Barkerville, B. C., August 2, 1934, and which repeated August 11, was caught by Mr. E. D. McKee at Grand Canyon, Arizona, February 4, 1935, and repeated February 5, 6, 8, and March 22 and 24, 1935. Of different significance is the record of another bird whose breeding ground is not known. This bird, a migrant male, was banded April 28, 1927, at Indianpoint Lake. It repeated on April 30. In 1934 it was caught April 20, at Kitimat Mission at tidewater, west and only slightly north of Barkerville. It would appear that this bird in its 1934 migration was following a different route from that of 1927. Such variation in route might well lead to different breeding grounds and on occasion lead to intermixture of races. Although it might be argued that this individual could travel west from Barkerville, it is improbable that it would travel almost directly west across migration routes and the formidable coast ranges. This bird was at least eight years old at the time of its last capture, a fairly long life span under normal conditions for a small bird of this type.

Relationships with adjacent forms.—For *J. hyemalis hyemalis* and *J. hyemalis cismontanus*, see pages 328–343.

J. oreganus shufeldti.—The southern division of *montanus* approaches *shufeldti* only in central Oregon. There is a belt no less than 30 miles in width along the Deschutes and Crooked rivers and Bear Creek that is not suitable for breeding juncos. This barrier would seem to be quite effective, inasmuch as populations on either side of the Deschutes River at Bend (Ochoco Ranger Station, and Cascade Mountains 16 miles west of Bend) show no evidence of intermixture, but are entirely characteristic of their respective races.

Montanus as a whole is of course only about 80 per cent differentiated from *shufeldti* in wing and tail length, which are the best characters. But the southern division also has average color characters (pale head and type 3 back) which reach an extreme in east-central Oregon and maintain this with no diminution westward to the barrier. The head color, although it averages slightly darker in males at Ochoco Ranger Station, averages paler in females (see figs. 10 and 19). These fluctuations are best ascribed to sampling. With the addition of color characters, more than 90 per cent of the individuals of the populations on either side of the barrier at Bend can be distinguished. Nevertheless, the few atypical individuals in each race make it impossible to maintain that the two do not occasionally exchange individuals in this region.

The Boreal area of the Paulina Mountains, east of the Cascades and south of Bend, is completely connected with the Cascade region by suitable junco habitat. Although it is separated from the Blue Mountain area, across the Crooked River, it is faunally and spatially the region closest to the breeding range of *montanus*. The birds of the Paulina Mountains are essentially *shufeldti,* but they show some intermediate features.

The available sample consists of 17 males and 3 females. Head color averages 3.68 (3.91, west of Bend; 5.40 at Ochoco Ranger Station). Back varies from type *t* phaeomelanin to type 2, average 1.06 (west of Bend, *t*–3, average 1.16; Ochoco, 1–3, average 2.80). In color, then, the sample is typically *shufeldti* and shows no influence of *thurberi,* the characters of which appear not far to the southward.

Measurements in which the races differ in the southern region are those of wing, tail, and middle toe. The first two are much more decisive than the third. Paulina birds are definitely intermediate in wing length (see fig. 12), though closer to *shufeldti.* The variation is only slightly greater in the intermediates. Tail averages 67.5 mm.; 67.1 in birds from west of Bend, 70.7 in birds from Ochoco. Middle toe (11.34) is equivalent to the average for *montanus.* Bill measurements average distinctly small (length 7.98 mm., width 5.66), smaller than in either race or than in *thurberi–shufeldti* intermediates to the south. This feature can only be characterized as a local variation of the colony.

The intermediacy of the Paulina group is not one which clearly results from exchange of racial characters across the barrier. It is not even certain that there has been any significant mixture, for if there had been, the color characters should reflect it. Certainly the coloration of *montanus* would not be completely selected out in this comparatively arid forest habitat, which resembles that of the interior mountains quite as much as it does that of the coast. There is no evidence that *shufeldti* coloration is dominant over that of *montanus.* If the population resembles *shufeldti* because of the complete contact with that race and the continual influx of individuals from it, why does not wing length correspond equally? I conclude that the group has had a *shufeldti* ancestry and as a somewhat isolated group has been altered subsequently with respect to wing and tail, as so many interior forms are, in association with the more open habitats and the severe winter conditions which impose greater need of extensive migration. The intermediacy thus is the result not of interbreeding, but of an intermediate type of environment.

Montanus and *shufeldti* meet in southern British Columbia. Breeding habitat is continuous from interior localities such as Clinton and Lillooet southwest through the mountains to the coastal mainland at the mouth of the Fraser River. Measurements of birds from intermediate localities either are lacking or are too few to indicate the nature or exact locus of the intergradation. Observation and data from specimens indicate that probably there is intergradation in the region between Lillooet and Chilliwack. The birds of the Okanagan area that belong with the southern division of *montanus* show no diminution in wing suggestive of *shufeldti.* Southwestward into Washington there may be sufficient continuity of habitat to allow considerable intermingling.

The extent of intergradation northward in the coast ranges of southern British Columbia is not known, inasmuch as the exact northern limits of *shufeldti* have not been reliably established in this area. Intermediates between *J. o. oreganus* and *montanus* have much in common with *shufeldti* and *shufeldti–montanus* intergrades; in fact, they may be identical genetically even though they are of different history. Very probably, therefore, in the coast ranges there are continuous and similar populations in a north–south line which to the southward are *shufeldti* but which farther north one would view as intermediates of *oreganus* and *montanus.*

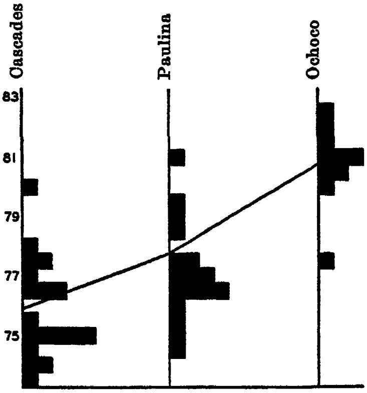

Fig. 12. Intergradation in wing length of males between *J. o. shufeldti* (Cascades) and *J. o. montanus* (southern division). Cascade sample from vicinity of Bend, Oregon. (Not spaced to scale geographically; see map, fig. 14.)

May not *shufeldti* have arisen from interbreeding of *montanus* and *oreganus?* I think this improbable in view of the range of *shufeldti,* which is situated too far to the southwestward. More likely, in view of the glacial history of the region, *shufeldti* of Oregon and Washington was the parent type, with *montanus* a larger interior counterpart. The small red *J. o. oreganus* differentiated in the northern coastal district. *Montanus,* in invading the interior with the glacial retreat, either through differentiation (see p. 257) or possibly through increments from *shufeldti,* gave rise to a slightly differentiated northern division. When the northern interior and northern coastal types met at the time of exposure of the high coastal mountains, they resynthesized *shufeldti*-like populations as intermediates geographically and structurally; there was rebuilt a similar genetic mosaic.

The high individual variability in color in *montanus* and *shufeldti* may be due to a crowding together during periods in the Pleistocene of stocks already somewhat diverse which failed to reassort upon expansion northward. The ruddier backed extremes of *shufeldti* seem associated to some degree with the humid coastal conditions on the Olympic Peninsula. Yet the mixture of this type with gray-backed birds both in the Puget Sound area and in the drier interior range of *montanus* suggests a shuffling of originally more uniformly differentiated races. Both long-time alterations in range through glaciation, and annual intermingling and straying in migration, have been factors.

J. o. oreganus.—Information is limited on the intergrading of *montanus* and *oreganus*. The sector of the coastal region from Queen Charlotte Sound to the Portland Canal is the region of contact. Exclusive of the Queen Charlotte Islands far off shore, breeding *oreganus* from this part of the coast are at hand from Calvert Island and from the vicinity of Princess Royal Island and the adjacent mainland. Many of the Calvert Island birds are somewhat intergradient toward *shufeldti*. A small series from Bella Coola may be taken as indicative of the intergradation of *J. oreganus* and *montanus* even if the former exists in submaximal form in this latitude. Calvert Island is somewhat south of Bella Coola, but a continuous waterway leads southwestward from Bella Coola to the island. The Princess Royal region is to the north and the mountains of the mainland are continuous with those of the interior at Bella Coola.

At the town of Bella Coola, McCabe found breeding juncos scarce; he encountered only a few in open timber above the valley floor and a few up the river to the eastward. These are not typical *J. o. oreganus,* although tidewater extends inland to this point. It appears, therefore, that *oreganus* is limited to the coastal lowlands west of the higher mountains, and does not in unmixed form extend to the head of such extensive inlets. Four birds, 2 males and 2 females, from localities ranging from Bella Coola to 18 miles east of Bella Coola, have the following back types: *oob* (1), *ob* (1), and 1*b* (2) (see pp. 245, 271 for explanation of types of back color). Type *oob* is a red-backed variant that never occurs in unmixed *montanus,* and *ob* is known only in one instance from *montanus*. This occurrence was at Hazelton in the Skeena Valley, possibly even there the result of intermixture. Type 1*b* never occurs in true *oreganus*. The *oob* bird of Bella Coola is barely within the limits of this color class, as it approaches *ob*. Its wing and tail are average for *oreganus,* but the tarsus is below the minimum of that race. The sides are heavily colored, clearly showing *oreganus* influence. The *ob* bird is inconclusive with respect to measurements, falling in the region of overlap for the curves of variation for the two races. One of the 1*b* birds was mated with the *ob* bird. This 1*b* bird is of average *montanus* wing length, though not beyond the range of variation of *oreganus,* but the tarsus is 21.3 mm., an extreme almost never attained in *montanus*. The other 1*b* bird is below the minimum of *montanus* wing and even below the average of *oreganus*. The tarsus is average for *montanus*.

At Bella Coola, then, characters of both races appear, in average, or often extreme form, but independently assorted in individual birds. The small sample has much in common with *shufeldti–oreganus* intergrades from Vancouver Island with respect to color, inasmuch as similar color extremes are intergrading.

About 30 miles east of Bella Coola in the transmontane by-pass and in the heart of the coast range, transition toward interior biotic conditions is found, and before the watershed is reached (east of the highest peaks, as this is an antecedent drainage system) typically interior conditions prevail. Four birds from 30 to 50 miles east of Bella Coola on the coastal drainage are *montanus* with respect both to color and size. These have been combined for the purposes of analysis with a group of birds from along the divide at Anahim Lake and from the Rainbow Mountains. Although these birds are essentially *montanus,* they do depart from average *montanus* in the direction of *oreganus* in an interesting fashion.

The wing average of 77.11 mm. (11 specimens) is decidedly intermediate between the 78.46 of northern *montanus* and the 75.00 of *J. o. oreganus.* The tail also is shorter than in *montanus,* but not to so great a degree. Upon studying individual wing lengths, it is seen that the lower average is not due to the presence of any very short-winged birds such as would suggest *J. o. oreganus* mixture, but that it results from a lack of the larger variants which contribute to the average of typical *montanus.* The types of back color occur: 1, 2, and 3 in the ratio of 9:0:2. The average is 1.3 compared with 1.9 in *montanus* to the eastward. The average is not much different from that of the Hazelton series, yet has fewer examples of types 2 and 3. Here, as in wing length, certain *montanus* variants (gray backs) have dropped out, but no *oreganus* variants have been added. This stage in intermediacy is thus very different from that along the lower Bella Coola Valley. An intermixture of *oreganus* and *montanus* types would probably increase variability in some characters after the first generation and something approaching the parental *oreganus* coloration should appear by segregation. Therefore this sample seems to be one representing a gradient in differentiation, not intermixture. This gradient may be merely a further manifestation of the dropping out of gray-backed types northwestward through *montanus.* But since it is coupled with shorter wing, one wonders if proximity to the coast may not in some manner influence the population and cause the dropping out of variants most unlike *oreganus.* This would be differentiation *in situ* in response, at least indirectly, to environment.

At Bella Coola there is interbreeding which results in high variation and in the appearance of extremes of character. The *montanus* variants found there do not surpass the extremes of the Anahim–Rainbow Mountain group. Thus, in this sector of the coast there are nicely demonstrated two kinds of intergradation, hybridization and intermediate differentiation. Earlier I indicated that the intergrades of the coast ranges have much in common with *shufeldti.* The back, for instance, averages 1.3 in both *shufeldti* and the Anahim Lake group. The fact that the wing is longer at Anahim, much as in *montanus,* shows that the history of the back in the two groups is not the same, but probably was arrived at independently.

At Swanson Bay on the mainland opposite Princess Royal Island, McCabe took five juncos near timber line, 4000–5000 feet. Four of these are of back type 1*b* or 1*a,* one is *ooa.* In size these birds correspond with *oreganus* of this vicinity from the outer coastal islands and from near sea level along the inlets. These birds are quite as intermediate as those of the Bella Coola area with respect to coloration. Although this small group does not conclusively show other intermediate features, it is difficult to explain the coloration except as diffusion westward of the interior type of back through the continuous mountains of the coast ranges.

This group of five is especially significant in comparison with birds of the very different lowland forest habitat at Swanson Bay. Eight birds taken from near tidewater, either here or on the outer islands, have among them but a single 1*a* variant. A zonal and associational difference correlates with back differentiation. The lowland habitat consists of muskegs in the timber, or the open parklike forest of the outer coast. Between the open outer coast and the balsam scrub of timber line is the heavy impenetrable forest at the base of high mountains unsuited to juncos and invaded by them only by means of occasional openings.

Junco oreganus shufeldti

This race occupies the coastal regions of Washington and Oregon and, even in extreme populations, is not fully differentiated from *montanus*. Yet, its divergence from this race is greater than the difference between the two divisions of *montanus*. *Shufeldti* is only partly migratory.

Racial characters.—*Shufeldti* differs from *montanus* in shorter wing and tail (average 4 per cent). Males of *shufeldti* are usually (75 per cent) less than 77 mm. in wing length; males of *montanus* usually (85 per cent) more than 76 mm. in wing length; females of *shufeldti* less than 73 mm. (66 per cent); *montanus* more than 72 mm. (85 per cent). By using these measurements, one can separate 75 to 80 per cent of the individuals of the two geographic groups. Similar limits could be set for tail length, but they would be less reliable because of greater individual variation (see table 20, p. 265). *Shufeldti* is similar to northern *montanus* in average head color, but the ruddier 1*b* type of back is more prevalent. Tail pattern, side color, and other measurements are similar.

Shufeldti differs from *J. o. oreganus,* as does *montanus,* in the grayer, browner, or less reddish hues of the back that never are the Prout's brown, Brussels brown, or raw umber of *J. o. oreganus*. Other average characters of *shufeldti* are less rufescent, often less dusky, sides, greater amount of white in the tail, especially in rectrices 4 and 5 (see p. 272), and shorter tarsus and toes (3 to 5 per cent).

For characters that differentiate *shufeldti* and *thurberi* see page 276.

Nongeographical variation.—The high variability of coloration in *shufeldti* is comparable to that in *montanus*. Only back color shows any average geographic modification within the race. Head color, classified as in *montanus,* averages 3.8 with variations from 1 to 6 (p. 247). Side color is of types 1 and 2 (p. 248). The brown overcast on feathers of the head, a phase of retarded plumage, is comparable in appearance to that found in northern *montanus*. There are no instances of white wing coverts. Mixed patterns in the ventral part of the hood occasionally occur in females. Sexual dimorphism and seasonal alterations are comparable to those in *montanus*.

Tail pattern for males is tabulated on page 253. It is similar to *montanus* in the kinds of variants present. Averages for the fourth rectrix and the inner web of the fifth fall closer to those of the northern division of *montanus;* those for the outer web of the fifth are closer to those of the southern division. Interracial differentiation is thus less than intraracial differentiation in *montanus.*

Variations and correlations are similar to those obtaining in southern *montanus* except for tarsal length, which is more variable. The high coefficient for tarsus seems to result from a peculiarly short-legged group from the Cascade Mountains near Bend, Oregon. This local variation may be without significance, as only 12 males were available. In any event, it bears no relation to any extensive geographic trends. Sexual dimorphism in wing and tail is 5 and 6 per cent, respectively, but it is lacking in bill and feet, except for bill length (2 per cent); this situation is similar to that in *montanus.* Tail is 12 per cent shorter than wing, as in *montanus.*

TABLE 20

MEASUREMENTS OF J. O. SHUFELDTI

Measurement	Sex	No. of specimens	Mean with prob. error	Standard deviation	Coeff. of var.
Wing..............	♂	64	75.65 ± .14	1.71	2.26
	♀	24	71.83 ± .22	1.60	2.22
Tail..............	♂	56	67.14 ± .18	2.03	3.02
	♀	24	62.58 ± .29	2.12	3.38
Bill length.........	♂	63	8.22 ± .03	0.36	4.42
	♀	23	8.03 ± .05	0.36	4.58
Bill depth..........	♂	57	5.89 ± .02	0.27	4.65
	♀	22	5.84 ± .04	0.28	4.75
Tarsus.............	♂	67	19.82 ± .05	0.64	3.20
	♀	24	19.59 ± .09	0.68	3.49
Middle toe.........	♂	65	11.50 ± .04	0.43	3.78
	♀	25	11.49 ± .06	0.42	3.67
Hind toe...........	♂	67	7.99 ± .03	0.38	4.79
	♀	25	8.02 ± .06	0.45	5.59

Geographical variations within the race.—Ruddier types of back are more common in the population of the Olympic Peninsula than in other sections of the race. That this is a result of exchange of breeding birds between the Olympic Peninsula and Vancouver Island, where a decidedly reddish *oreganus*-like population of intergrades exists, is doubtful. If such exchange is a common occurrence, why are not the populations of the adjacent mainland of southern British Columbia also involved? The increase in ruddiness is coincident with a more humid habitat which is not unlike that on parts of Vancouver Island. It is not impossible that the slight average difference between the birds of the Olympic Peninsula and those of the section of Washington lying immediately east of Puget Sound is due to the less frequent penetration into the extreme coastal regions of strays of *montanus* type from the interior. The graph (fig. 13) shows the contrast of southern *montanus* and *shufeldti* in Oregon and the slight intraracial variation in *shufeldti* with respect to depth and amount of phaeomelanin pigment. Male *shufeldti* are usually of type *b* back (eumelanin intensity) as in northern *montanus.* However, in the northern half of Oregon about 50 per cent are type *c*. This condition in combination with types 1 or 2 of phaeomelanin means the birds resemble the duller variants of *thurberi*. This tendency to diminish eumelanin is more and more apparent along the gradient toward *thurberi* in southern Oregon; it is not the influence of *montanus*.

The wing, tail, bill, and middle toe all average somewhat smaller throughout coastal Oregon than elsewhere in the race (fig. 18). This is not related to the gradient running south into *thurberi*, although *thurberi* may maintain some of these lower values along the coast. The coastal group of the Olympic Peninsula shows none of this diminution.

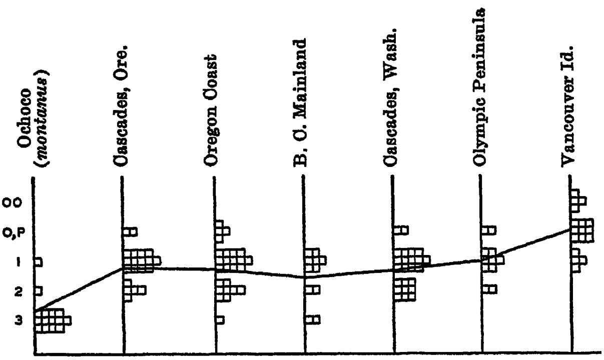

Fig. 13. Occurrence of back variants (phaeomelanin) in males in samples of *J. o. shufeldti*, in *montanus* adjacent to *shufeldti*, and in *shufeldti-oreganus* intergrades from Vancouver Island (not spaced to scale geographically). Line connects averages for samples. For explanation of variants see page 247.

Distribution in the breeding season.—The race occurs in coniferous forests of the coastal mainland west of the more arid interior slopes of the coast range in British Columbia, and in Washington and Oregon west of the Columbia River plains and the Deschutes–Crooked River–Bear Creek drainage. It occurs south to Coos, northwestern Douglas, Lane and western Deschutes counties. Beyond these points the gradients in characters in the direction of *thurberi* become more pronounced. Distribution is nearly continuous in these areas, except in parts of the Willamette Valley.

The northern limit of *shufeldti* has not been precisely determined. There are specimens from Howe Sound just north of Vancouver, B. C. From Lund, about 80 miles northwest of Vancouver, a single male bird shows some approach to *oreganus*, as does also a bird from Johnstone Strait. It has been pointed out that *shufeldti*-like birds appear in the coast range farther north but that they are intergrades between *montanus* and *J. o. oreganus*.

The most common forest type in this region is the *Pseudotsuga–Thuja plicata–Tsuga heterophylla* combination, with local areas of mountain hemlock (*Tsuga mertensiana*) and fir and, on the coast, Sitka spruce. As a whole the forest habitat is much like the humid cedar-hemlock forests of northern Idaho that are occupied by populations of *montanus*. But climatic conditions are somewhat milder, and, perhaps as a result, there is less migration on the part of the juncos. The birds breed from sea level to timber line at 5000 to 7000 feet in the Cascade Mountains.

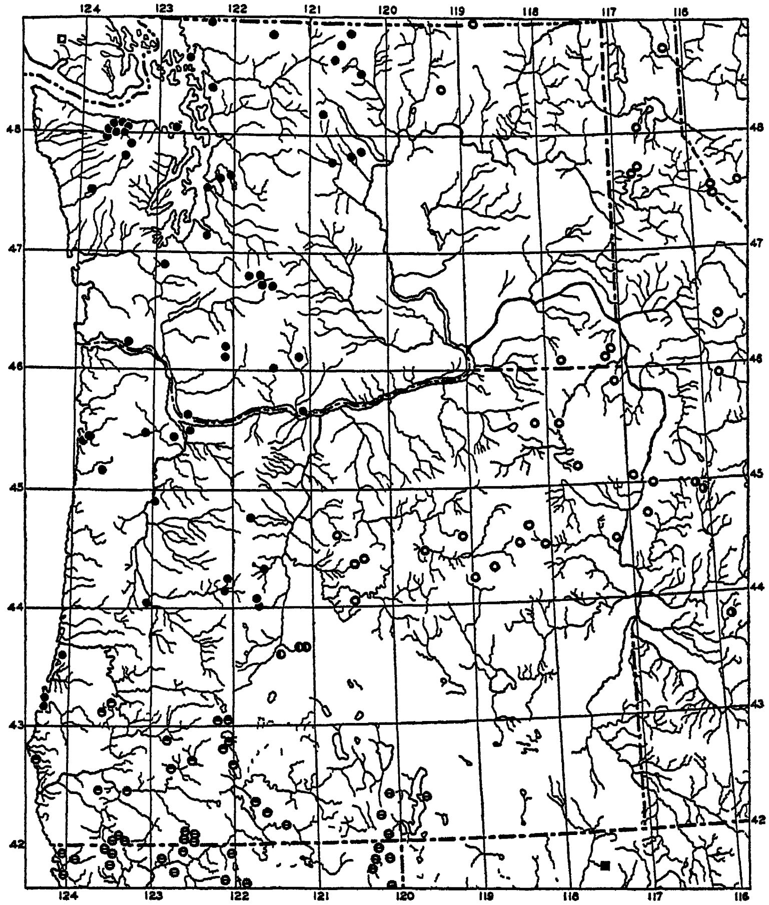

Fig. 14. Distribution of breeding juncos in Oregon and Washington, and portions of neighboring states. Each symbol represents a locality from which specimens have been examined. Dots, *J. o. shufeldti;* plain cirles, *J. o. montanus;* half dots, left half solid, intermediates between *J. o. shufeldti* and *J. o. montanus;* half dots, upper half solid, distinctly intermediate groups between *J. o. shufeldti* and *J. o. thurberi;* half dots, right half solid, intermediates between *J. o. montanus* and *J. o. mearnsi;* circle with cross bar, *J. thurberi;* square enclosing white dot, intermediate between *J. o. shufeldti* and *J. o. oreganus;* solid square, *J. o. caniceps.*

Distribution in winter.—Occurs commonly at lower altitudes within the breeding range, north to the lower Fraser River, British Columbia, and throughout coastal Oregon and Washington. It also occurs fairly commonly in northern and central California, but rarely east of the Sierra Nevada or south to the San Diegan district and northern Lower California. The extent to which this race moves eastward to winter in the interior is difficult to determine. As explained on page 258, identification of individuals of *montanus* and *shufeldti* of back types 1 and 2 is not possible without data on measurements, which in some of my earlier work were not obtained. Study of large series of wintering birds from Arizona now at hand reveals that only a few fall below the minimum size limits of *montanus*. Others might be either small *montanus* or large *shufeldti*. Along with the type of *shufeldti* from New Mexico there are a few other specimens which on the basis of size or extreme coloration (type *o* back) must certainly have originated within the breeding range of *shufeldti*. These have been taken in Arizona, New Mexico, Nevada, Utah, and eastern Colorado. Strays may occur in the northern states of Mexico and in western Texas, but satisfactory determination of these has not as yet been made. The names *shufeldti* and *couesi* previously employed by me in studying certain collections apply, for all the latter and for most of the former, to the interior type of Oregon junco which now properly bears the name *montanus*. Inability to allocate all records of Oregon juncos from the southern Rocky Mountains and desert areas should not confuse the general situation, which can be stated with assurance, namely, that true *shufeldti* is a rarity east of the Cascade–Sierra Nevada mountain system, just as is *thurberi* in that area, and that the largest part of the *shufeldti* population winters within the breeding range of the race and in California.

Relationships with adjacent forms.—For *J. oreganus montanus* and *J. oreganus thurberi*, see pages 258 and 286, respectively.

J. oreganus oreganus.—It may be said that the juncos of the immediate coastal belt show a gradient from Oregon to Alaska in which the phaeomelanin of the back and sides and the size of tarsus and feet increase to the northward. Also there is some increase in eumelanin and diminution in white areas in the tail. The gradients in back color and tarsus, the most pronounced ones, do not coincide in detail; the chief increase in redness takes place farther south than does the elongation of the tarsus. Irregularities in the steepness of the gradients make it possible to fix racial limits arbitrarily (see locality lists and ranges), yet *shufeldti* and *oreganus* and their intermediates should really be viewed as a unit.

Figure 15 shows the gradient in redness of the back, with a distinct break at the Straits of Juan de Fuca between the Olympic Peninsula and southern Vancouver Island. Fully as pronounced a break occurs between the mainland of British Columbia and Vancouver Island (compare graph, fig. 13). The Vancouver Island group is predominantly of type *o* back, which is rare in *shufeldti*, *oreganus*, and *montanus*. Yet there are among the Vancouver Island males at least four that are indistinguishable from *shufeldti* and five that fall well within the limits of *oreganus*. Swarth (1912, p. 59) noted this resemblance to *oreganus*, but he rather overemphasized it because he considered extremely gray interior birds to be typical *shufeldti*. The next station that is at all well represented is Calvert Island. The island lies in the northern coastal faunal area, where conditions are much colder and rainfall heavier than on southern Vancouver Island. At this point the backs show another distinct advance in redness; they average nearly as red as in *oreganus* of Alaska and the Queen Charlotte Islands. Whether the increase occurs gradually or abruptly, perhaps at the north end of Vancouver Island where it is suspected that biotic conditions are more like those of Calvert Island, is not known. Two birds from Johnstone Strait are of back types *oo* and *o*.

The next series of birds to the northward is one from the vicinity of Princess Royal Island, British Columbia. Excluded from this group are some birds of intermediate character taken in the mountains of the mainland which show intermediacy with *montanus*. Even without these, the group interrupts, slightly, the increase in ruddiness to the northward. This effect, if it is not the result of sampling, might well be associated with the more interior situations from which the birds come. Calvert Island is distinctly more coastal in aspect than the inner side of Princess Royal Island. This section of the coast has the maximum of rainfall found along the coasts of southern Alaska and British Columbia. Possibly the high occurrence of *a*-type back (rich in eumelanin) in this sector is associated with the heavy rainfall. This is a deviation quite independent of the degree of ruddiness.

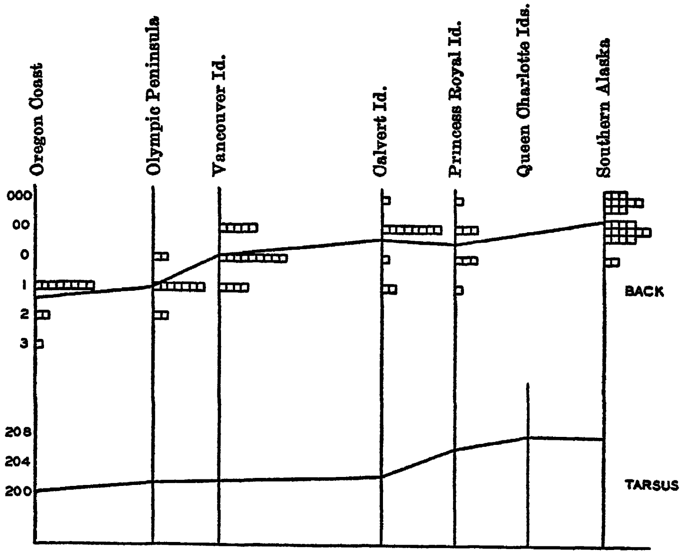

Fig. 15. Noncoördinated geographic variation in back color (phaeomelanin) and tarsal length in males along the Pacific coast from Oregon to southern Alaska. Groups spaced to scale geographically. Lines connect averages.

From the southern boundary of Alaska northward, no intensification in *oreganus* characters occurs. The birds of the Queen Charlotte Islands are like those of Alaska, but not enough information is at hand to permit entering them on the graph.

The tarsal measurements show a very slight increase, uniform in rate, north to Calvert Island. Between there and Princess Royal Island a sudden increase occurs. The two gradients (color and tarsus) are thus independent and not susceptible to exactly the same geographic barriers and biotic changes, as, for example, at the Straits of Juan de Fuca. The reliability of the average for Calvert and Princess Royal birds is felt to be reasonably good. Females and males are combined by adding to the average of the females the normal sexual difference in Oregon juncos. The distribution of individual variants is such that the average appears to be reliable.

The Vancouver Island series appears to have sides not appreciably richer in color than *shufeldti,* but in the Calvert Island birds and those from farther north the color is that of true *oreganus.* The average amount of white in the tail of the Vancouver Island group is distinctly intermediate between *oreganus* and *shufeldti* (for details see table, p. 272). The Calvert Island and Princess Royal groups are not quite equal to *oreganus.* The average for head color of males from Vancouver Island is 3.6, which compares with 3.2 in *oreganus* and 3.8 in *shufeldti.*

The independence of gradients in character and the extended zone of intermediacy without increased variability suggest that the intermediacy results from progressive differentiation in association with geographic and environmental factors. There nowhere appears to be a group produced by intermingling and hybridizing of the racial extremes.

Junco oreganus oreganus

The humid coast belt from Yakutat Bay, Alaska, south to Queen Charlotte Sound, British Columbia, a region strongly characterized ecologically, is occupied in the breeding season by this race, which is the terminal differentiate of the species in the north. *J. o. oreganus* shows several features which seem related to conditions peculiar to this area and which parallel differentiations in other endemic birds of the region. The race is only partly migratory.

Racial characters.—Features which distinguish *J. o. oreganus* from *shufeldti* and *montanus* are given on pages 264 and 252. In summary, *J. o. oreganus* is short winged and short tailed like *shufeldti;* the phaeomelanins and eumelanins are intensified, especially the former, so that the back and sides are more ruddy and the head, sides, and back are darker on the average. The tarsus and toes are longer and heavier. Back color alone effects a 92-per cent segregation of *oreganus* and *shufeldti* and a 97-per cent segregation of *montanus.* Wing and tail length also permit an 80-per cent segregation of *montanus,* and tarsal length, to a nearly equal degree, sets *oreganus* off from both its conspecific neighbors. Other features are more purely matters of average.

Features which differentiate *J. o. oreganus* and *J. hyemalis cismontanus* are given on page 343.

Nongeographical variation.—Variability in coloration in *oreganus* is great, as in *montanus* and *shufeldti.* None of the colors shows intraracial geographic variation apart from the gradient in back coloration already discussed (see pp. 268 and 269).

Head color, classified as in other races, varies from type 2 to type 6, but averages 3.2 instead of 3.8 and 4.0 as in *shufeldti* and northern *montanus.* These classifications are made by inspection of the ventral surface of the hood. The pileum in *oreganus* seems to be relatively darker so that in the lighter categories, 4, 5, and 6, the pileum is more as in 3, 4, and 5 of *montanus.* Thus, the heads actually average darker than the indices show.

Back types *o, oo,* and *ooo* of *oreganus* are stages in phaeomelanin intensification and produce progressively more reddish color. Almost all *oreganus* are of types *oo* and *ooo,* neither of which occurs in adjacent forms. The eumelanin varies in intensity, producing variations in blackness or darkness of the red. Two categories, completely intergradient, were established. Type *a,* the blacker variant, is about as prevalent as *b* in males. In females type *a* is almost lacking. Categories *a* and *b* are comparable, but not equal, to types of eumelanin in *montanus,* in which the eumelanin is less completely mixed and, in the darker types, forms large gray basal areas on each feather vane. The eumelanin of *oreganus* is deposited throughout the vane in the barbule tips. The occurrence of categories *a* and *b* is not in any way correlated with types *oo* and *ooo.* The averages for the latter are the same in males and females. Intensity of head color and eumelanin of back are not correlated. The interrelation of pigments is thus decidedly different from that in *montanus,* in which back types *b* and *c* and head are correlated. The fact that eumelanin is largely in the basal parts of the back feathers of *montanus* and not so much mixed with phaeomelanin in the tips indicates that different mechanisms are involved; different correlations naturally result. However, there is some correlation between head color and phaeomelanin of the back. This also is true to some degree in northern *montanus* and probably in *shufeldti.* Why these two should be associated is not clear, since different pigments are involved. If the correlation were a matter of maleness, or retarded or progressive plumage, one would expect females to differ from males in the phaeomelanin of the back. Instead, they are deficient in eumelanin of the back, which in *oreganus* is not correlated with ruddiness. The association of head and phaeomelanin may represent a linkage of characters, and may not be brought about because of similar physiologic processes involved in the production of the pigments.

Side color is chiefly of two types: *a,* with relatively unmixed phaeomelanin, equivalent to type 2 in *montanus* but with extension of the area as in type 3 and with redder phaeomelanin (always a little eumelanin present); and *b,* with distinctly more eumelanin, comparable to extremes of type 1 of *montanus* but with phaeomelanin redder and hence total effect less vinaceous and closer to burnt umber. A third, distinctly sooty type, with the phaeomelanin materially obscured by eumelanin, was found in two breeding birds only. This variant almost suggests hybridization with *hyemalis,* but I believe it is independent of this, as one such bird came from Sitka. The chief intraracial variation consequently is one of the eumelanin component. Types *a* and *b* are about equally represented, type *a* being somewhat more common. There are no fewer type *b*'s in females. Eumelanin of the sides is in no way correlated with head pigmentation.

Buff feather tips are less prevalent than in *montanus* and *shufeldti,* yet some extremes occur. Their association with sex and age applies in the same fashion as in *montanus* (see p. 252). The buff tippings of the nape are usually more ruddy in this race. No instances of mixed phaeomelanin and eumelanin in the ventral part of the hood have been found. There are no instances of white on the wings or of red on the pileum deeper than the feather tips.

The only aspect of wear that is different from that in other Oregon juncos relates to the back; there the darker red brightens very materially from the Prout's brown of fresh feathers, but never becomes yellowish or whitish along the edges of the feathers as in *shufeldti, thurberi,* and *montanus.*

TABLE 21

OCCURRENCE OF RECTRIX PATTERN IN J. O. SHUFELDTI AND J. O. OREGANUS (IN PERCENTAGES)

	Males			Females
	J. o. oreganus	Intermediates from Vancouver Is.	*J. o. shufeldti*	*J. o. oreganus*
Rectrix 4				
Inner web:				
pure black	56	35	17	86
trace of white	33	59	44	11
mixed	10	6	40	3
Outer web:				
pure black	91	88	62	97
trace of white	4	6	15	3
mixed	4	6	19	0
trace of black	0	0	2	0
pure white	0	0	2	0
Rectrix 5				
Inner web:				
mixed	37	26	10	78
trace of black	42	23	42	19
pure white	20	50	48	3
Outer web:				
pure black	11	0	0	31
trace of white	6	0	0	22
mixed	54	50	17	39
trace of black	22	18	17	8
pure white	7	32	67	0
Rectrix 6				
Inner web:				
mixed	0	0	0	3
trace of black	6	0	0	31
pure white	94	100	100	66
Outer web:				
mixed	0	0	0	6
trace of black	1	0	0	8
pure white	99	100	100	86

Sexual dimorphism in the color of the head is higher in *oreganus* than in southern *montanus,* in keeping with the trend of modification seen in *mearnsi* and *montanus,* in which the female lags behind in the increase of blackness. In southern *montanus* the average sexual difference of the ventral surface of the head is 2 (♂ 6, ♀ 8), in *oreganus* 3 (♂ 3.2, ♀ 6.2, both darker dorsally).

In *shufeldti* the dimorphism also appears to be high, but the representation of females is not entirely adequate. A slight sexual difference in average back color with less eumelanin in the back of females has been noted. This is comparable to that in *montanus.*

Oreganus lacks variants with white or nearly white outer webs of the fifth rectrix, but has new variants with pure black and nearly pure black outer webs of the fifth rectrix and with mixed webs of the sixth rectrix. Throughout the rectrices, average increase in black is to be noted relative to *shufeldti* and northern *montanus. Oreganus* is an extreme in this respect that parallels in an interesting fashion the southward increase in black among the yellow-eyed juncos of Central America. In both, the increase accompanies general increase in eumelanin in body plumage, though the latter is vastly different in the two series. The tail markings and the head or other body areas are not correlated in individual variation within a population, but the interracial correlation is striking. Sumner has found similar conditions involving color areas in *Peromyscus.* The difference in tail pattern between *oreganus* and *shufeldti* or between *oreganus* and *montanus* (northern) is greater than that between *shufeldti* and *montanus* or between the two divisions of *montanus.* It is about equal to the difference between *mearnsi* and northern *montanus.* Sexual dimorphism is apparent in all vanes of the outer three feathers.

TABLE 22

MEASUREMENTS OF J. O. OREGANUS

Measurement	Sex	No. of specimens	Mean with prob. error	Standard deviation	Coeff. of var.
Wing	♂	74	75.00 ± .14	1.81	2.41
	♀	38	71.02 ± .18	1.67	2.35
Tail	♂	74	66.13 ± .16	2.11	3.19
	♀	35	62.58 ± .27	2.43	3.88
Bill	♂	71	8.18 ± .03	0.32	3.93
	♀	33	8.21 ± .03	0.22	2.73
Bill depth	♂	64	5.77 ± .03	0.30	5.30
	♀	33	5.83 ± .03	0.27	4.67
Tarsus	♂	75	20.72 ± .04	0.57	2.74
	♀	38	20.35 ± .07	0.63	3.08
Middle toe	♂	65	11.98 ± .05	0.58	4.83
	♀	38	11.76 ± .06	0.54	4.56
Hind toe	♂	75	8.37 ± .03	0.39	4.66
	♀	39	8.15 ± .07	0.53	6.51

Coefficients of variability are similar to those for *montanus* and *shufeldti,* except that those for middle toe are higher. The coefficients for tarsus are low as in *montanus,* not as in *shufeldti.* Sexual dimorphism is 5 to 6 per cent in wing and tail and, unlike the situation in *shufeldti* and *montanus,* is definitely present (2 per cent) in the feet; it is lacking in the bill. Tail is 12 per cent shorter than wing, as in *shufeldti* and *montanus.* Correlation of wing and tail is .717 ± .038, comparable to that in other northern juncos, though a little higher than in *montanus.* Thirteen males from the central British Columbian coast average 18.4 gr. in weight, compared with 17.7 gr. for 100 *montanus*. If the figure for this small sample should hold true for all *oreganus*, we would have a clear case of reduced wing and increased body size. Certainly from the evidence of weight and large feet it is difficult to conceive of *oreganus* as a smaller bird than *montanus*. It must be a less able flier. In this connection are to be noted the less extensive migration of *oreganus* and the less open character of the forests in its breeding and wintering ranges.

The coefficient of correlation for tarsus and hind toe is low and uncertain; tarsus and middle toe show a coefficient of .407 ± .066, and middle toe and hind toe, .301 ± .069. Although correlations of foot parts are erratic in all races of juncos, they are always slightly positive. It is perhaps significant that in several forms with large feet, compared with related races, tarsus and toe correlations increase materially. This is so in *oreganus*, and it is exactly paralleled in *alticola*, which is large footed in comparison with its Mexican relative *J. phaeonotus*.

Geographical variation within the race.—Once the full development of *oreganus* characters is attained in the Queen Charlotte Islands and in southern Alaska, no further change occurs to the northward. Birds from various divisions of the coastal archipelago, the outer islands, the mainland, the northern section around Glacier Bay, and the Queen Charlotte Islands were analyzed separately without positive results. The occasional duller variants from the coastal mainland, especially from the mouths of rivers draining from the interior, suggest intergradation and intermixture with *montanus* and *cismontanus* (see pp. 262 and 337).

Distribution in the breeding season.—The race breeds in the humid coastal district from Yakutat Bay south through the Alexander Archipelago to the Queen Charlotte Islands. In an easterly direction it ranges to the mainland coast, at least at low elevations, but extends inland no farther than the tidal inlets and lower river valleys; in some instances intergradation begins at these latter points. On the mainland it extends south to Princess Royal Island, British Columbia. At Calvert Island decided modification of certain characters is found, although the birds are still in most respects like the more northern populations; south of Queen Charlotte Sound intergradation is marked.

Juncos in much of this area are sparsely distributed, probably because of the prevailing density of the forest and undergrowth. They occur chiefly along the borders of muskegs, meadows, streams, and beaches and in the occasional tracts of parklike timber, especially on the outer islands. Cedar (*Thuja*), Sitka Spruce (*Picea sitchensis*), and western Hemlock (*Tsuga heterophylla*) dominate the forest. There is an abundance of epiphytic growth. No other junco experiences more overcast weather and precipitation during the breeding season. The sun may be obscured from view for many days in succession. Nearly all the occupied region is below 2000 feet in elevation. Some of the higher mountains of the islands may afford suitable junco habitat at timber line.

Distribution in winter.—The lowest mean monthly temperature at Sitka is 33°. This is indicative of the winter conditions which permit this race to winter, at least occasionally, as far north as this point. Little snow falls in the lower parts of the breeding area. Migration is therefore quite irregular. Yet, probably the majority of the birds move south, many wintering in western Washington and Oregon and intermingling with those members of *shufeldti* which fail to migrate. *Oreganus* ranges south in winter regularly to central California, particularly the coastal district. Winter distribution has been based on unequivocal specimens only, those closely corresponding to the *oo* and the *ooo* types of back of the breeding season. There are substantiated records for New Mexico (Fort Bayard), Idaho (Nampa), Nevada (Carson and Ruby Lake), Arizona (Phoenix, Fort Verde, and the Huachuca Mountains), and Lower California (Santa Eulalia). These are the only certain records outside of western Washington, Oregon, and California, except for British Columbia and the breeding range. They represent less than 3 per cent of the winter-taken *oreganus* which I have examined. There are a few record

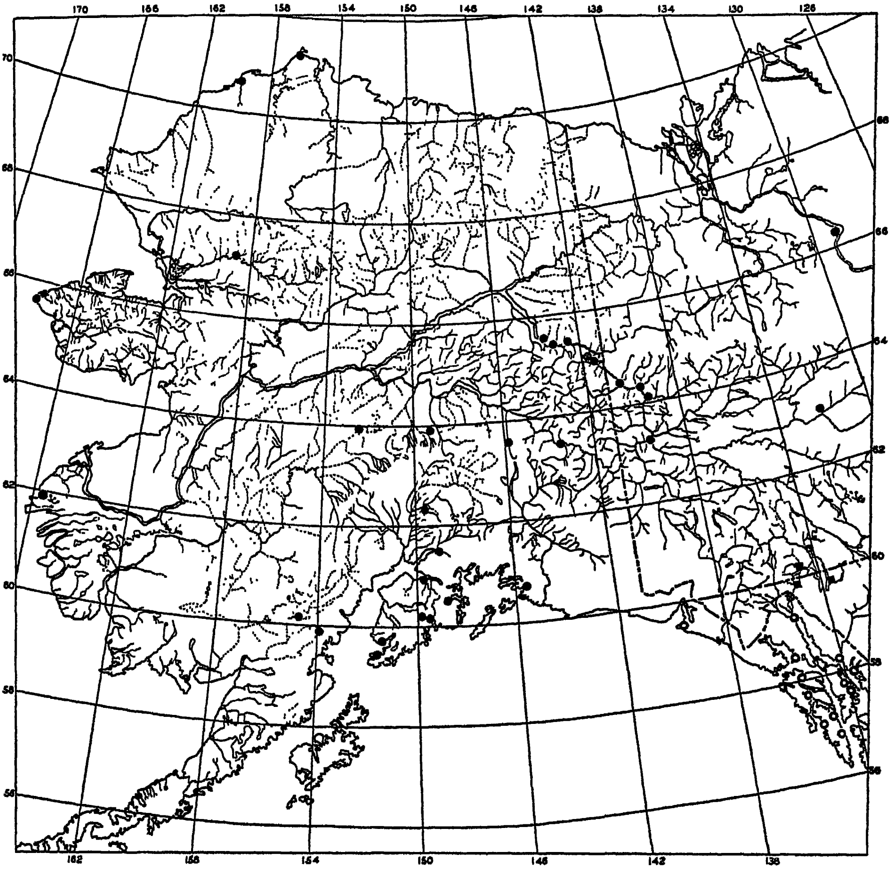

Fig. 16. Distribution of breeding juncos in Alaska and parts of northwestern Canada. Each symbol represents a locality from which specimens have been examined. Dots, *J. h. hyemalis*; circles, *J. o. oreganus*; solid squares, *J. h. cismontanus*; half solid square, intermediate between *J. h. hyemalis* and *J. h. cismontanus*; circles enclosing crosses, hybrids between *J. oreganus* subsp. and *J. hyemalis* subsp.

stations along the Sierra Nevada, and in southern California on Santa Cruz Island and at Temescal. From the Monterey Peninsula northward along the Pacific coast, occurrence is much more regular. That *oreganus* migrates into the interior with regularity is evidenced by a number of specimens from the Okanagan region of British Columbia taken in midwinter. Winter stations in the breeding range include, beside Sitka, the Queen Charlotte Islands, B. C., and Wrangell, Alaska; at the last-named two places a number of examples have been taken.

The remarkable adherence of *oreganus* to humid forested areas in winter is highly suggestive of its preference and possible adaptation for comparable environments in summer. To a less degree this same tendency is seen in *shufeldti*. There is enough movement inland to indicate that it is not impossible, so far as migration routes and barriers for both these races are concerned, for them to spread to inland desert areas in winter. I believe it is preference for, or adjustment to, specific conditions in southerly latitudes which are most similar to those of their breeding habitat that largely determines the wintering range. The lesser power of flight of both compared with *montanus*—a condition frequently associated with denser floral habitat—may be an important factor.

Relationships with adjacent forms.—For *J. o. shufeldti*, *J. o. montanus*, and *J. hyemalis* subsp. see pages 268, 262, and 329, respectively.

Junco oreganus thurberi

This race, like *montanus*, is a complex one with incipient subdivision and numerous gradients in characters traceable within it. Several geographically variable characters grade south into and through it from *shufeldti*. Yet there is a mixture of pigments in the back that is found widely and almost exclusively in *thurberi*. This pigmentation becomes prevalent in the vicinity of the California-Oregon boundary and may be employed arbitrarily as a key character to delimit the races. Except for a few outlying areas, the breeding range comprises two tongues of the Transition and Boreal zones that extend southward in California. The larger of these is that of the southern Cascade–Sierra Nevada mountain system, which is extended discontinuously by the mountain-top Boreal "islands" of southern California. The smaller area includes the coastal regions of northern California south through Sonoma County. The two areas are extensively joined through the Shasta region, but the differentiation of the two groups of birds associated with them is greater than that within the long interior range from Lassen County to San Diego County.

Racial characters.—*Thurberi* is most completely differentiated from *shufeldti* by the lighter, more pinkish back. The color is Verona (fresh plumage), snuff, Sayal, or mikado brown, rather than the bister (fresh plumage), sepia, or Saccardo's umber of *shufeldti*. This difference permits 90-per cent segregation of individuals in the interior ranges, 75-per cent along the coast. The difference is the result of diminution of eumelanin in the barbule tips with unmasking, and increase of, phaeomelanin in *thurberi*. The latter pigment is of a pale yellowish type, different from that of *J. caniceps* but apparently not distinct qualitatively from that of the backs of other Oregon juncos. Sides are nearly lacking in eumelanin; phaeomelanin is restricted to extreme lateral regions; the color is near avellaneous and vinaceous buff instead of army brown, fawn color, or vinaceous fawn.

Other characters of *thurberi* such as slightly darker head and longer wing and tail (2 per cent) hold only for the Sierran division. The amount of white averages greater on rectrices 3, 4, and 5.

For characters which differentiate *thurberi* from *J. o. pinosus* and *J. o. pontilis* see pages 290 and 299, respectively. *Thurberi* does not meet *montanus,* a hiatus existing between their ranges in southeastern Oregon. The same color differences that distinguish *shufeldti* from *thurberi* distinguish *thurberi* from *montanus* even more sharply. Moreover, the head of southern *montanus* is a much duller black.

Nongeographical variation.—Most of the variable characters show some geographic correlation, so that all measurements and the colors of head, back, and tail are best discussed later. Color abnormalities are limited to white wing spots, which occur in about 1 per cent of the thousand birds examined. Pileum overcast with brown is found as in all Oregon juncos, but it is less prominent than in *montanus* and *shufeldti.* There are no instances of reddish pileum and few of interrupted hood margin. Individual variation in coloration of the sides is insignificant. Wear and fading may alter the back color decidedly. The dilute eumelanin of this race seems especially susceptible to fading so that the back becomes much brighter, and more yellow or tan in late summer. The exposure to intense light in parts of the breeding area, as compared with the exposure in more northern habitats, may accelerate fading of eumelanin and brightening of the phaeomelanin. The color of the sides becomes faint and is inconspicuous in badly worn plumages.

Sexual difference in head color is variable within *thurberi;* in the north it is equal to that in *oreganus* and in *shufeldti,* but it diminishes southward. The backs of females average somewhat lighter, that is, they have less eumelanin. The difference in sexes in other Oregon juncos is comparable with respect to eumelanin. The sides are similar in the sexes. Tail pattern differs in the average on rectrices 3, 4, and 5. The degree of difference is roughly comparable to that in *J. o. oreganus* and *montanus.* In *oreganus* rectrix 3 is not involved, owing to absence of white, but the variable sixth rectrix shows average difference.

Geographical variation within the race.—In *thurberi* white spotting appears occasionally on the third rectrix. This was not found in the coastal forms to the north and but rarely in *montanus;* the percentage in *thurberi* is not quite as great as in *mearnsi.* White or nearly white inner webs of the fourth rectrix appear as variants in this race. Aside from these, the classes of variants in *shufeldti* and *thurberi* are the same. Averages for white areas in rectrices 4 and 5 are higher in *thurberi* than in *shufeldti.* The differences are somewhat greater than those between southern *montanus* and *mearnsi,* or between the divisions of *montanus* and *shufeldti,* but not so marked as between *oreganus* and its neighboring races. A parallel between tail white and light coloring of sides and back with respect to the race as a whole is apparent, but, as in other such parallelisms, individual variation of the characters is not correlated. Unlike *mearnsi* and *J. o. oreganus,* in which similar parallelism is evident, *thurberi* has a darker head than *shufeldti* coincident with a tail that is whiter.

TABLE 23

OCCURRENCE OF RECTRIX PATTERN IN J. O. SHUFELDTI, THURBERI, AND PINOSUS (IN PERCENTAGES)

	Male			Female	
	shufeldti	*thurberi* (Tahoe)	*pinosus*	*thurberi* (Tahoe)	*pinosus*
Rectrix 3					
Inner web:					
trace of white	0	11	0	0	0
Rectrix 4					
Inner web:					
pure black	17	3	43	4	54
trace of white	44	19	49	42	43
mixed	40	66	8	54	3
trace of black	0	6	0	0	0
pure white	0	4	0	0	0
Outer web:					
pure black	62	15	72	36	95
trace of white	15	12	18	12	0
mixed	19	27	7	30	5
trace of black	2	18	2	14	0
pure white	2	28	2	8	0
Rectrix 5					
Inner web:					
mixed	10	0	36	2	54
trace of black	42	3	38	18	35
pure white	48	97	26	80	11
Outer web:					
pure black	0	0	3	0	8
trace of white	0	0	8	0	16
mixed	17	1	26	6	43
trace of black	17	3	18	10	14
Outer web:					
pure white	67	96	44	84	19
Rectrix 6					
Both webs:					
pure white	100	100	95	100	86

The independence of these several characters, physiologically and genetically, suggests that such parallelism as is evident results from similar selective agencies working upon the different parts of the organism.

The values for tail white in the table are representative of the Sierran-southern Californian division of the race. In the coastal division certain parts of the tail pattern average the same as in *shufeldti* or *shufeldti–thurberi* intermediates of extreme northern California. The independence of the white spotting on different webs, even of the same feather, is manifest with respect to geographic gradients. Individually within a population there is correlation of markings in several of the feathers of the tail. For example, in 100 males from the Tahoe sector correlation of amount of white in the two vanes of the highly variable fourth rectrix is .531 ± .049; for white of the outer vanes of rectrix 4 and 5, .620 ± .06. Correlation of inner web of rectrix 5, which has a small variation, and outer web of rectrix 4 is lower (.336 ± .06), yet it is probably significant. In working this latter correlation it was noted that black-spotted fifth rectrices occurred only with black or nearly pure black fourth rectrices.

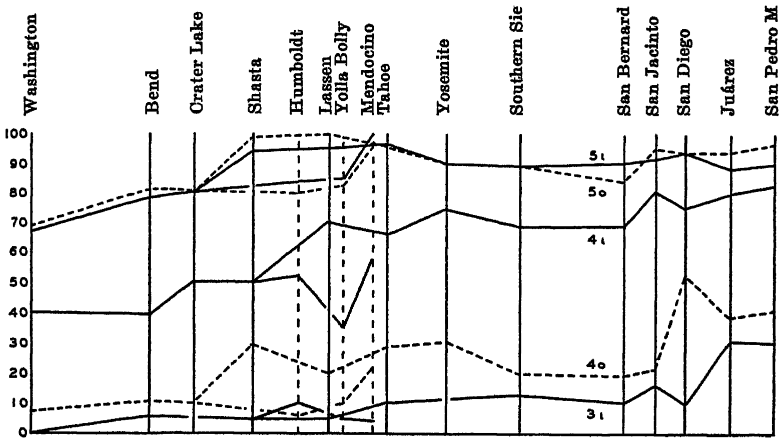

Fig. 17. Geographic variation in amount of white in tail along Pacific coast. Vertical lines represent samples spaced to scale geographically. Solid vertical lines mark positions of interior groups from the Cascades of Washington (*shufeldti*) to the Sierra San Pedro Mártir of Lower California (*townsendi*); broken vertical lines, groups of *thurberi* in coastal region of California. Figures at left represent percentage of occurrence of variants. *5i* and *5o*, inner and outer webs, respectively, of rectrix 5 pure white; *4i* and *4o*, webs of rectrix 4 mixed rather than black or chiefly black; *3i*, inner web of rectrix 3 with trace of white rather than pure black. Males only.

The graph (fig. 17) shows in the upper two lines the percentage of occurrence of pure white in the two webs of the fifth rectrix in different geographic groups from Washington south to Lower California. The geographic gradients of the two are closely related. The *thurberi* level is attained in the Siskiyou-Shasta region with no significant alterations thereafter. The Crater Lake and Bend samples are intermediate. The correspondence of these trends is not a result of linkage of these characters. No correlation individually exists between the two vanes of this feather. (This does not mean that when greater amounts of black are present on this feather, as occurs in other forms of juncos, correlation individually does not exist.) Increase in white southward along the coast is shown by branch lines. The Mendocino and Yolla Bolly groups retain the intermediate values of the Crater Lake sample, and only in the terminal area of the coastal region is a level comparable to that of the Shasta region attained. The modification is thus retarded southward on the coast and a long region of nearly perfect uniformity is established at the level of the intermediate group of the interior. Southern coastal Oregon birds are similar to Washington *shufeldti.* The ultimate increase in white along the coast is not a result of *pinosus* influence.

The two vanes of the fourth rectrix show an interesting independence. The outer vane attains a level in the Shasta district that, with some irregularities, is maintained south to the San Jacinto Mountains. The extreme increase in San Diego County is a departure in the direction of the Lower California forms, but because other characters show no such resemblance this may be merely a local modification. The pronounced change in value in the north occurs between Crater Lake and Shasta. The Crater Lake group, unfortunately small, corresponds perfectly with *shufeldti* of the Cascades to the northward. On the inner web, white does not attain a *thurberi* level until the Lassen district is reached. Even if the Crater Lake group be ignored, the large Shasta group is decisive. Thus the average for one web changes north of Shasta entirely; the other accomplishes two-thirds of the total alteration south of Shasta. The outer web corresponds with rectrix 5.

In the coastal district the outer web of rectrix 4 again parallels rectrix 5; in that region it is about equal to *shufeldti.* The inner web is variable, but resembles in general that of the Crater Lake and Siskiyou intermediates. A small sample from Del Norte County, California, and from adjacent Oregon has a somewhat higher average for white, but this deviation is reasonably attributed to the size of the sample. In the group from Coos County, Oregon, amounts of white are typical of *shufeldti.* The differences in trends occur in spite of correlation individually of the two webs. This situation is comparable to that in the wing and tail, characters which may become altered independently, as for example in *J. c. caniceps* and *dorsalis,* and yet are correlated within a population. There appear to be common factors controlling both webs of the fourth rectrix, yet also separate factors that may affect one web or the other alone.

White on rectrix 3, a variation which is absent in *shufeldti,* appears occasionally from Bend south through the Crater Lake, Del Norte County, and Lassen groups. Between Lassen and Tahoe a higher frequency of occurrence is reached, a point of change which corresponds not at all with that for either rectrix 4 or 5. On the coast a diminution from Humboldt County southward is found that reverses the trend in the other tail feathers and runs counter to the gradient in the Sierra. In other features of tail pattern the affinity of the Humboldt group appears to be with populations farther north; in this instance it is with the Tahoe group.

The population in the Warner Mountains, Lake County, Oregon, and Modoc County, California, is intermediate between the Crater Lake group and the Shasta group with respect to tail pattern.

In general the indices of variability and the correlations of dimensions are extremely similar to those of *shufeldti.* Tail variability, however, is distinctly lower. The coefficient of correlation of wing and tail in males is .637 ± .043, similar to that in *montanus* (and probably also *shufeldti*). No measurements other than wing and tail are correlated. Weight apparently is no more related to linear measurements of limbs than it is in southern *montanus,* where the relation could be adequately analyzed. Average weights are available only for the coastal division of *thurberi.* Sexual dimorphism in wing and tail is between 5 and 6 per cent. Difference in wing and tail averages 12 per cent as in related races. Sexual difference in bill length is 2 per cent, but there is none in bill depth and it is uncertain in the foot. This pattern of sexual differentiation is exactly as in *shufeldti.*

TABLE 24

MEASUREMENTS OF J. O. THURBERI
(Tahoe sector of Sierra Nevada)

Measurement	Sex	No. of specimens	Mean with prob. error	Standard deviation	Coeff. of var.
Wing	♂	86	76.81 ± .12	1.64	2.13
	♀	48	72.59 ± .18	1.85	2.55
Tail	♂	86	68.82 ± .14	1.99	2.89
	♀	42	65.34 ± .18	1.80	2.75
Bill	♂	84	8.04 ± .02	0.29	3.69
	♀	42	7.82 ± .04	0.35	4.47
Bill depth	♂	81	5.59 ± .02	0.26	4.65
	♀	43	5.64 ± .03	0.28	5.07
Tarsus	♂	95	19.64 ± .04	0.57	2.90
	♀	49	19.39 ± .06	0.64	3.31
Middle toe	♂	90	11.29 ± .03	0.41	3.66
	♀	48	11.31 ± .04	0.42	4.24
Hind toe	♂	95	8.09 ± .03	0.39	4.89
	♀	49	8.03 ± .04	0.39	4.88

Wing, tail, bill, bill depth, and middle toe show racial differences and intraracial trends that are comparable to those of the tail pattern in that there is lack of coincidence in some of the principal modifications. The graph (fig. 18) shows the average values plotted against miles in a general north–south direction for each adequately represented breeding population. Wing and tail lengths increase to the southward between central Oregon and Tahoe, and then maintain a fairly uniform level. Average wing length alters abruptly between Shasta and Lassen, the tail over a much greater distance. Nevertheless, the most important alteration in the tail lies in the same Shasta-Lassen interval. The continuation of the tail gradient upward from Lassen and Tahoe is probably only the effect of normal variation in samples. Likewise, the Bend group may not be significantly low; the Shasta average in reality is like more northern *shufeldti.* Therefore the difference in modification of wing and tail may be unduly emphasized by the graph.

Bill length shows an abrupt alteration between Tahoe and Yosemite. From Tahoe north, the value is essentially that of *shufeldti.* Bill depth declines between central Oregon and Shasta, then abruptly between Lassen and Tahoe.

The latter is an alteration not paralleled in other characters except middle toe, which changes chiefly here from a high northern to a low southern average. An extreme southern diminution also occurs in middle toe length.

One feature of the curves is the uniformity in the Sierra south of Yosemite and as far as the San Gabriel Mountains. The isolated populations still farther southward give evidence of colonial variations, although they are no more isolated than the San Gabriel group. The three southernmost areas are all especially well represented, each having more than thirty breeding males.

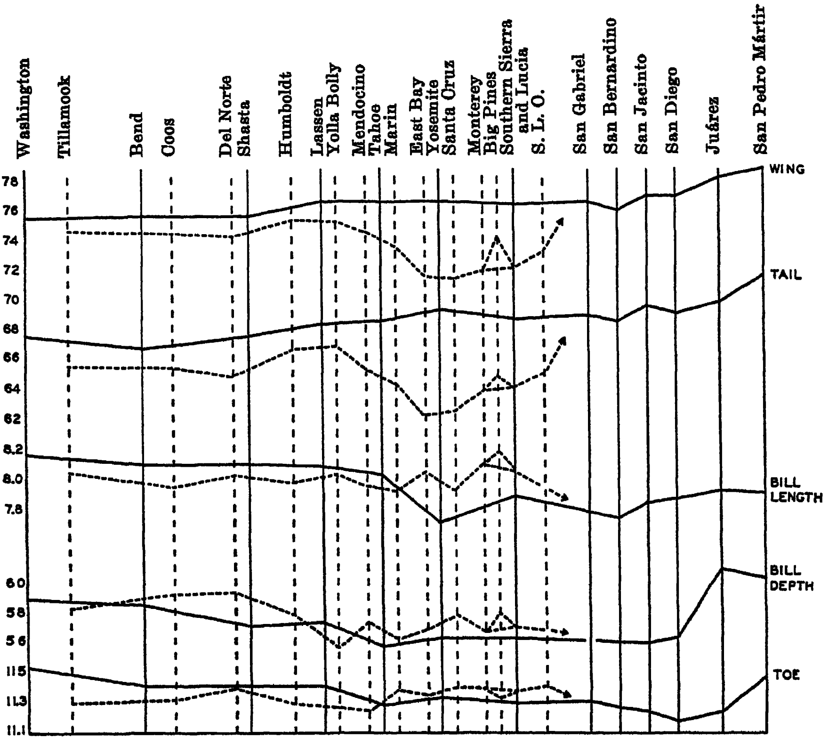

Fig. 18. Geographic variation in averages of dimensions (mm.) along the Pacific coast. Samples spaced to scale geographically. Solid lines, interior groups from the Cascades of Washington (*shufeldti*) to the Sierra San Pedro Mártir of Lower California (*townsendi*); broken lines, coastal groups from Oregon (*shufeldti*) to central California (*pinosus*). Males only.

Twenty-four males from the Warner Mountains of Oregon and California correspond with Lassen males in wing length, being large, but they also are long billed like populations of central Oregon.

Upon the coast, wing and tail lengths increase, as compared with the slightly smaller coastal groups of *shufeldti,* but the increase may be the result of the interior position of the Mendocino and Yolla Bolly groups, not their more southerly positions. A diminution evident in the Mendocino coastal area may be part of a gradient carried on into *pinosus,* or merely a return to a general level for the immediate coastal strip. As is true for most features of tail pattern, the coastal group is related to the southern Oregon populations, and in this instance to the Shasta population also.

Bill length in the coastal region again preserves a value typical of coastal *shufeldti,* though it is close also to the Shasta-Tahoe value. Bill depth south of Del Norte County is variable, but most like that of the Lassen group, except for the Yolla Bolly population, which drops to the level of the Sierran groups south of Lassen. Middle toe is short throughout as in coastal Oregon and the Sierra Nevada. Except for bill depth the coast population clearly shows affinities with the birds of coastal Oregon or with those of northern interior California.

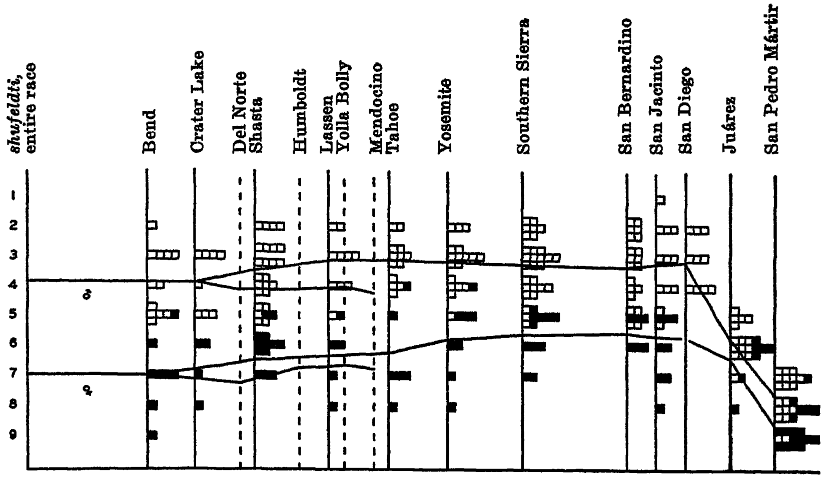

Fig. 19. Geographic variation in head color along the Pacific coast. Individuals represented by squares; open squares, males; solid squares, females. Samples spaced to scale geographically. Solid vertical lines interior groups from *shufeldti* of Washington to *townsendi* of Lower California; broken lines, groups of *thurberi* from coastal section of California. For explanation of variants see page 247.

Weights of thirty-five breeding males are available from the Mendocino and Humboldt districts. The average is 17.58 gr., compared with 17.72 for southern *montanus;* coefficients of variability are 5.5 and 5.2, respectively. The difference in averages is but 0.7 per cent and is not significant. These same *thurberi* (also *shufeldti*) are 4 to 5 per cent shorter in wing and tail than *montanus.* The difference in the races is purely one of proportion of parts, therefore, and not a general difference in size.

Head pigmentation has been classified according to the same system as that used for *montanus,* only the ventral surface being considered. As in *oreganus* and to a less degree *shufeldti,* the categories are not, however, exactly the same as those of *montanus.* The intensities of melanin are the same, but the heads of *montanus* are more often ashy or bluish gray in the light gray variants, and in the coastal races they are sooty gray. Also, as in *oreganus,* the pileum normally associated with a given category is darker than in *montanus.*

Slight average increase in blackness takes place to the southward (see fig. 19). The principal change is in the Crater Lake–Shasta interval, with some increase thereafter to Tahoe. It should be noted that the range of individual variation is similar throughout, and that only a shift in proportion of types is involved. Extremes in *shufeldti* males are 1 and 6, in *thurberi* 1 and 5, except on the coast. The average is usually near 3.2; in *shufeldti,* 3.8.

On the coast, the *shufeldti* average is maintained southward to Sonoma County. The Warner Mountain group averages 3.4, the same as the Shasta birds; hence there is no intermediacy in the direction of *montanus.*

Sexual dimorphism in head color in *shufeldti* is about 3 in terms of head types. Females increase in blackness, as do males from Crater Lake to Shasta, with some increase on to Tahoe (see fig. 19). Unlike the situation in males, the increase continues from here through Yosemite so as to reduce the dimorphism to about 2½ south of this point. On the coast, dimorphism likewise diminishes from 3 to 2½, the females increasing in pigment, the males remaining constant.

In connection with other races of *oreganus,* it has been noted that dimorphism of the head appears to be correlated with progressive increase in black pigment. The females lag behind both in interracial differentiation (compare *montanus* and *oreganus*) and in hybrid intergradation. In a sense, then, females "catch up" with males in *thurberi.*

Analysis of back color is comparable to that made for other Oregon juncos. With regard to eumelanin, categories *b* and *c* occur which are quite comparable to those of other races; *b* is rare south of the intergradational area. Additionally, there is type *d* with even more reduced eumelanin. Beyond this, in the matter of pigment reduction, the variants lose eumelanin almost entirely from parts of the feather vanes. In worn plumage this produces a mottled appearance with light, bright areas dominating the back (type *dd*). This is the so-called mixed yellow of the *caniceps–thurberi* crosses. Its appearance rarely within the range of *thurberi* adjacent to the Great Basin would indicate some heterozygosity in the pair of factors, A A′ (see p. 194). If the mechanism is correctly hypothesized, occasional A′A′ or yellow (*y*) backs should appear where mixed yellows are moderately common. This is what happens in the San Jacinto Mountains, the only locality of occurrence outside of areas of obvious intermixture. Mixed yellow backs appear so much more ruddy or yellow than those with the *d* type of eumelanin that one is tempted to ascribe the effect to more phaeomelanin. Apparently, however, the color results merely from the complete unmasking of the phaeomelanin in certain areas. Mixed yellows are readily confused with badly worn backs of type *d* in which abrasion of the feathers causes resemblance to the normal areas of the mixed type that are without eumelanin.

Of the phaeomelanin variants, type 1 and occasionally 2 are found, but additional types with more phaeomelanin occur which are designated *t* and *p*. The series, 2, 1, *t, p,* represents in order simple increase in phaeomelanin. Class *t* may be essentially the same as class *o* of *shufeldti–oreganus* intergrades, but since it usually is combined with *c* or *d* eumelanin it produces a color much lighter, that is, more pinkish or tan. Because color under the microscope is difficult to evaluate, I hesitate to call *p* and *o* identical, although they would seem to be. Type *p* seems to be merely an additional stage of concentration and increase of phaeomelanin which, when combined with eumelanin of types *c* and *d,* appears ruddier than *tc* or *td.* Worn *p* types are often difficult to distinguish from *tdd,* owing to breakdown of the feather margins. Type *p* is one that occurs in *pinosus,* but within *thurberi* it is not limited geographically to intergradational areas.

Figure 20 shows the increase southward of phaeomelanin and the diminution in eumelanin. The changes in the two pigments are well coördinated. Between Bend and Crater Lake and again between Crater Lake and the Siskiyou-Shasta area major alterations occur, slightly the larger one in the former region. Warner Mountains birds are similar to those of Shasta.

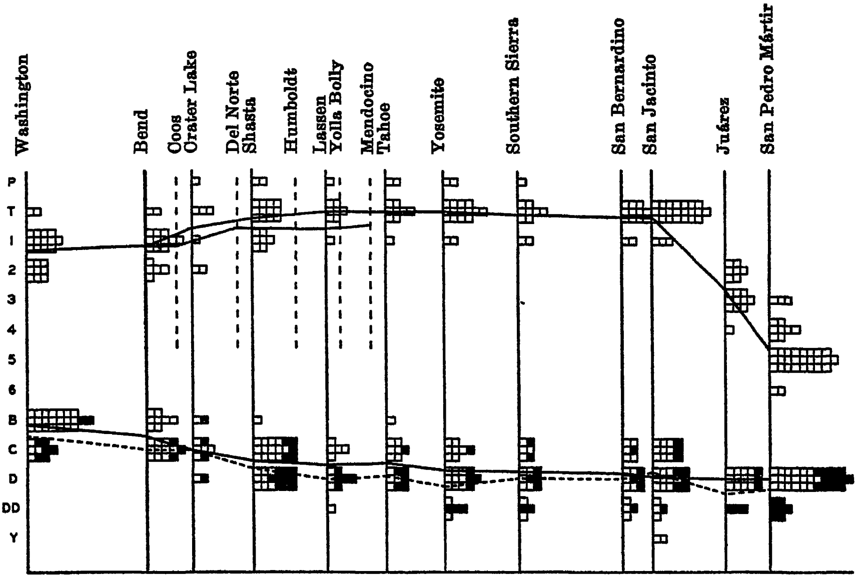

Fig. 20. Geographic variation in back color along the Pacific coast. Individuals represented by squares; open squares, males; solid squares, females. Vertical lines represent samples spaced to scale geographically. Solid vertical lines interior groups from *shufeldti* of Washington to *townsendi* of Lower California; broken vertical lines, groups from coastal Oregon and California. For explanation of variants see page 284. Upper section, phaeomelanin; branch line connects averages for coastal groups. Lower section, eumelanin; broken line connects averages for females.

These characters of the back are the most conspicuous ones with the sharpest geographic breaks; they are best used if a definition of racial limits is desired. Type *c* eumelanin and 1 phaeomelanin are found at both geographic extremes, but they are not often combined. There is no correlation of eumelanin and phaeomelanin in individuals. Using back color, a practical separation of the northern and southern interior groups to the extent of about 90 per cent may be made. The same series has been handled that Dwight (1918, pp. 293–294) used in estimating that only 80 per cent of El Dorado County breeding males, and less of females, are distinguishable from northern races. The higher percentage now attained is, I believe, attributable to better understanding of the variations of northern races and to the weighing of both phases of back pigmentation in the analysis. Females have been found to be as readily separable as males.

The sexual difference in the back is confined to the eumelanin. The broken line in figure 20 is the average value for females, with individual females shown by solid squares. The averages are generally, but only slightly, lower. A curve for phaeomelanin of females coincided so closely with that for males as to be impractical of representation.

On the coast the averages for back color change less abruptly to the southward and do not attain values equal to those of the Sierran division. They are similar to those of the Crater Lake intermediates. A 75-per cent segregation of coastal *thurberi* from *shufeldti* is possible on the basis of back coloration. (Individual variation is shown in fig. 23.) Types such as 2*c* and 2*d* are fairly common on the coast. These are almost lacking in *shufeldti,* so that there results an appearance of incipient differentiation of a sort not found elsewhere. But when it is considered that such a type as 2*d* is merely a combination of *shufeldti* and *thurberi* pigment, one hesitates to view the coastal tendency as a new departure.

In the southern section of the interior division the occurrence of types *dd* and *y,* which possibly have something to do remotely with *caniceps,* depress the eumelanin curve. The Modoc group averages the same as the Lassen sample.

Summary of geographic variation within the race and relationships with shufeldti.—Thurberi and *shufeldti* and their intergrades form a complex, with more or less continuous breeding range, through which run geographic gradients in characters which are not always correlated and which sometimes run counter to one another. The gradients are of differing steepness and regularity. Each population or colony may have an average genetic pattern more or less peculiar to it. The entire mosaic is at best only artificially subdivided into so-called races which have no high degree of unity. Races could be mapped out on the basis of one group of characters which would not coincide with races based on other characters. The selection of characters is arbitrary, and hence the races are man-made, not natural. If a point could be found where there was maximum change in several coördinated and well-marked gradients, this might be accepted as a natural dividing line. A satisfactory point of this kind has not been found, however.

No great discontinuity of breeding range occurs except south of the Sierra Nevada. Biotic differences are recognizable between Bend and Crater Lake, Crater Lake and Shasta, Shasta and Lassen, Lassen and the Sierra Nevada, and even within the Sierra. The tabulation shown on the following page is an attempt to outline the principal breaks in the curves for characters of male juncos in terms of faunal breaks or discontinuities in distribution (see map, fig. 21).

The contrast between birds of Mount Lassen and the Yolla Bolly Mountains on either side of the Sacramento Valley is considerable, and it is sharper than that between any other adjacent groups. Intervention of the noninhabitable valley and different environmental conditions in the two regions are associated with this contrast. Even so, this differentiation is not nearly so great as the changes occurring between Bend and Shasta, or Bend and Lassen. The changes in these intervals are of greater magnitude, are cumulative, and result in two fairly well-defined extremes.

OUTLINE OF BREAKS IN CURVES FOR CHARACTERS OF MALE JUNCOS IN TERMS OF FAUNAL BREAKS

Interval	Number of characters showing important change	Characters
Successive intervals in south to southeasterly direction:		
Washington–Bend, Oregon	2	Rectrix 5, eumelanin
Bend–Crater Lake	2	Eumelanin, phaeomelanin
Crater Lake–Siskiyou Mountains and Shasta	5	Rectrices 4o, 5, eumelanin, phaeomelanin, head
Shasta–Lassen	3	Rectrix 4i, wing, tail
Lassen–Tahoe	3	Rectrix 3i, bill depth, middle toe
Tahoe–Yosemite	2	Bill, eumelanin
Yosemite–southern Sierra Nevada	0	None
Southern Sierra–San Gabriel (discontinuity)	0	None
San Gabriel–San Bernardino (discontinuity)	1	Wing
San Bernardino–San Jacinto (discontinuity)	3	Rectrix 3i, wing, tail
San Jacinto–San Diego (discontinuity)	2	Rectrices 3i, 4o
Intervals in general southerly direction on coast:		
Coos County–interior Humboldt Co. (intervening area in Oregon and Del Norte Co. poorly represented)	6	Rectrix 5, rectrix 4i, wing, tail, bill depth, phaeomelanin
Humboldt–Yolla Bolly Mountains	3	Rectrices 3i, 4i, bill depth
Yolla Bolly–Mendocino and Sonoma counties (coasts)	6	Rectrices 4o, 4i, 5, wing, tail, bill depth
Intervals in general east–west direction		
Bend–Coos Co. (southwest)	5	Rectrix 5, 4i, wing, tail, eumelanin
Shasta–interior Humboldt Co.	7	Rectrices 3i, 4o, 5, middle toe, head, eumelanin, phaeomelanin
Lassen–Yolla Bolly Mountains (discontinuity)	8	Rectrices 4i, 5, wing, tail, bill depth, middle toe, head, phaeomelanin

It can be concluded that the principal modifications occur at several points in southern Oregon and northern California in regions where there is nearly continuous breeding distribution. Color characters as a group change north of the point where size characters change. The coastal division of *thurberi* resembles the populations of southern Oregon in many respects, either because of continuity, or because of similarity of environment, or both. Regional differentiation in the whole complex appears in the absence of physical barriers to breeding distribution, but where there are environmental differences. Such differentiation is sometimes absent where there is isolation. The barrier of the lower Sacramento Valley doubtless is important in maintaining extremes on either side that are developed in the course of the extensive regions of diverse but habitable nature that indirectly connect them.

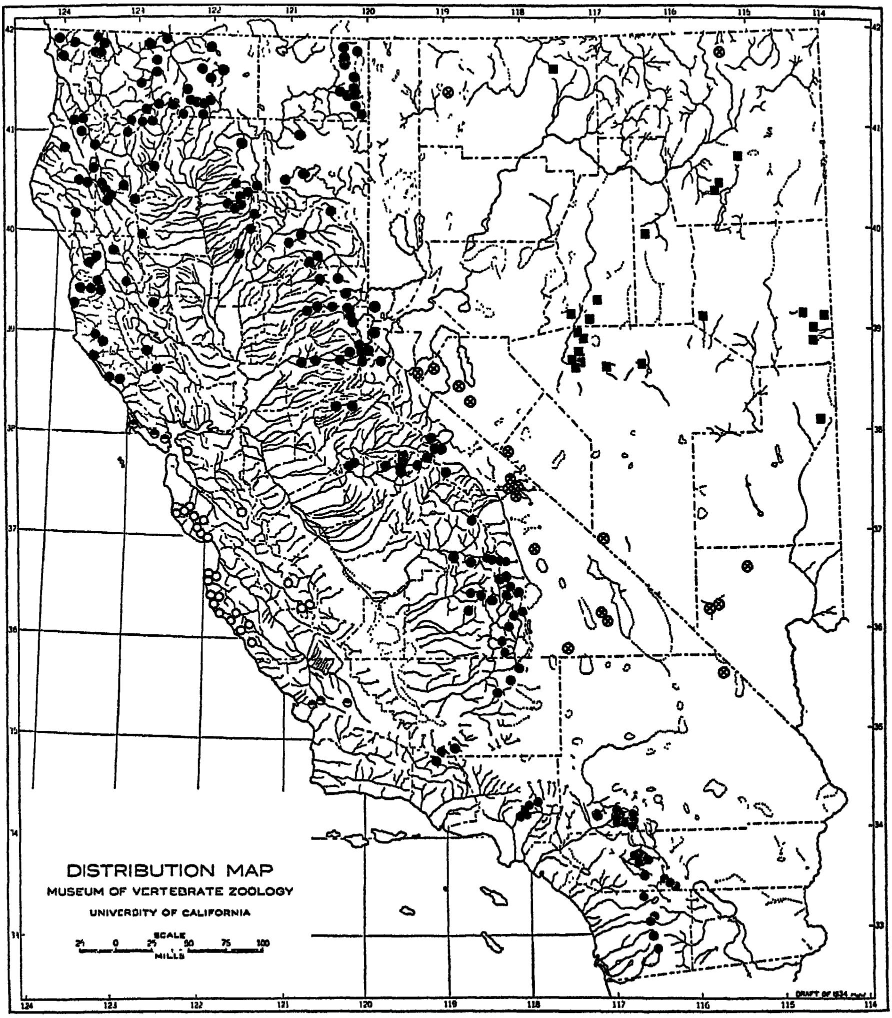

Fig. 21. Distribution of breeding juncos in California and Nevada. Each symbol represents a locality from which individuals have been examined. Dots, *J. o. thurberi;* circles enclosing crosses, hybrid groups involving *J. o. thurberi* and *J. c. caniceps*, and in northeastern Nevada, *J. o. mearnsi* and *J. c. caniceps;* squares, *J. c. caniceps;* circles, *J. o. pinosus;* half dots, intermediates between *J. o. thurberi* and *J. o. pinosus.*

Distribution in the breeding season.—Intermediates are distributed continuously south from Coos, northern Douglas, Lane, and Deschutes counties in Oregon to the California line. If for cataloguing purposes it is essential to name intermediates, the Crater Lake district and the area just south of the Rogue River may be taken as the northern regions for application of the name *thurberi.* Distribution in this sector extends from the coast to the Warner Mountains, with local discontinuity in Klamath and Lake counties. The Warner Mountain colony is isolated to the southwest from the Shasta and Lassen districts.

In California, distribution of intermediate and fully differentiated populations is coextensive with the Transition and Boreal forests of the Cascade-Sierran system, south to Walker Pass and the Kern River. From there south, *thurberi* is found in isolated areas of coniferous timber as follows: Piute Mountains, Kern County (a specimen from Fort Tejon, Kern County, may actually have been taken in the higher mountains near there); Mount Pinos, Fraser Mountain, and probably Cobblestone and Pine mountains, Ventura County; San Gabriel, San Bernardino, and San Jacinto mountain systems (including Santa Rosa Mountain); Santa Ana Mountains, Riverside and Orange counties; and in San Diego County from Palomar Mountain to the Laguna Mountains. On the coast in the north, distribution is continuous from Del Norte County to central Sonoma County and in the interior south along the mountains to northern Napa County. Marin County birds and those from San Luis Obispo County show affinities with *pinosus* of the central coastal district. Birds east of the Sierra Nevada show the result of mixture with *caniceps,* although they are principally of *thurberi* character.

Coniferous forests are the usual habitat throughout the range. Moist places, especially meadows, are preferred but are not required. Suitable ground cover consisting of grass and low herbage is most often found in such places, or in open or down timber, or along a forest edge. In places on the coast, madrone and oak timber, usually along a stream, may be inhabited, and in southern California and in the interior nesting pairs are occasionally found in the deep canyons among golden-cup oaks and alders. The dense redwood forests of the north coast are uninhabited, but the edges of such timber are used. On the coast there are great areas where the population is sparse.

A marked contrast is apparent between the forests of the interior and southern ranges and those of the coast of California. The former are relatively arid in summer but support a Boreal flora that is dependent on the winter snow pack. The coastal district, for the most part of lower elevation, is more humid in summer, more subject to summer rains, and more nearly uniform in daily range of temperature. Only certain higher parts of the coastal region are snow-covered in winter. Much difference in the herbaceous plant cover results which might be of significance to breeding juncos. The altitudinal range of *thurberi* is great, extending from sea level to timber line at 9000 to 11,500 feet. The lower limits rise in the interior and to the southward to about 4000 feet with the retreat upward of the Transition Zone.

Distribution in winter.—Migratory movements are variable, some individuals staying on or near the breeding grounds, as in the north coast district, whereas others move considerable distances into Arizona and northern Lower California. The majority winter in the foothill and Upper Sonoran areas of the Pacific slope of California. Unquestionable specimens of *thurberi* have been examined from Siskiyou County that were taken in midwinter, and intermediates like those breeding in southern Oregon occur in the Klamath and Rogue river drainage basins of that state.

East of the Sierra Nevada the proportion of *thurberi* in winter flocks is not high. There are a few records from north of Owens Valley, as at Eagle Lake, Lassen County. Along the bases of the mountains they are often plentiful, but they are rare in the desert ranges farther east. In Arizona, specimens have been examined from the vicinities of Flagstaff and Prescott and from the Chiricahua and Huachuca mountains. Strongly characterized birds from the latter range demonstrate that at least some of the Arizona records of *thurberi* are not based merely on aberrant members of more northern races. *Thurberi* is to be expected as an occasional visitor throughout the parts of Arizona suitable for wintering juncos.

From Colorado (Golden) and northern New Mexico (Charma) I have examined one bird each that might be referred to *thurberi*. In view of the overlapping of racial characters, these are not considered sufficient to warrant the conclusion that these areas constitute part of the wintering territory of the race. Southwestern New Mexico is undoubtedly visited occasionally by *thurberi* (one record, Big Burro Mountains, Grant County).

In Lower California, *thurberi* ranges southward on the west coast and in the San Pedro Mártir district to about latitude 30°. There are a few records for the Colorado Delta region. The occurrence on Guadalupe Island of some Oregon junco (Bryant, 1887, p. 299) can never be substantiated, owing to loss of the specimen; therefore it seems hazardous to assign the record to any particular race. *Thurberi* has been taken on several of the islands off southern California.

Relationships with adjacent forms.—For *shufeldti* see the foregoing discussion, pages 277–286. For *pinosus* see page 295.

Junco oreganus pinosus

Pinosus is a well-differentiated race that is sharply defined geographically. Discontinuities in distribution between it and *thurberi* are not greater, nor are they attended by greater environmental changes, than those that occur within the range of *thurberi*. The characters of the race are not the culmination of gradients that extend southward along the coast, but often represent reversals of these trends. The area occupied is the coastal region from San Francisco Bay south through Monterey and San Benito counties to San Luis Obispo County. The race is not limited to the true coastal forests of the Monterey region, but inhabits a great diversity of biotic situations, displaying a tolerance for low zonal conditions not found in *thurberi*. The race is nonmigratory.

Racial characters.—*Pinosus* is differentiated from *thurberi* by its ruddier back and sides. Back russet (fresh plumage) or cinnamon brown (worn plumage) instead of the Verona (fresh plumage), snuff, Sayal, and mikado browns of *thurberi*. Exceptions to this characterization amount to less than 10 per cent in *thurberi,* 25 per cent in *pinosus.* Sides near Sayal brown and cinnamon, although more dilute and not identical with these colors. Sides resemble less vivid types of *mearnsi.* Such color is almost never found in *thurberi* and is lacking in less than 5 per cent of *pinosus.* Head color of males lighter in *pinosus* (average 6, instead of 3 to 4), but there is 33 per cent of overlapping with coastal *thurberi.* Reduction in sexual dimorphism of head in *pinosus* involves maintenance of pigment intensity in females nearly equivalent to that of *thurberi.* Wing and tail much shorter in *pinosus* (6 and 7 per cent), but even so there is some overlapping with *thurberi.* Bill length, bill depth, and middle toe length average slightly (1 to 2 per cent), but consistently, greater. Tail pattern with less white, the averages approaching, but not quite equaling, values for *oreganus.* The averages are closer to *oreganus* than are those of *shufeldti.*

Nongeographical variation.—Head types of males are 5, 6, and 7. These are identical with similarly designated variants in the western races of *Junco oreganus.* The range of variation is less than in *thurberi* (1–5). The females vary more than males, ranging from 5 to 9. The average is about 7.5, compared with 6 for males. The net dimorphism thus is 1½, whereas it is 3 in *shufeldti* and 2½ in southern *thurberi.* Dimorphism follows the general rule according to which less sexual difference occurs in lighter-headed races. *Montanus,* with a head average of 6 in males, shows a sexual difference of 2.

Back color with respect to phaeomelanin is either of type *t* or *p,* but more commonly the latter. Both these categories occur in *thurberi.* The difference in *pinosus* is one of relative abundance of the two types (see fig. 23). There are some *pinosus,* however, in which the intensity is more extreme than in any *thurberi* of type *p;* but the difference is not such as to warrant establishing an additional category. Under the microscope the greater amounts of phaeomelanin in the barbules in type *p* may readily be seen. As in other Oregon juncos, females show no higher frequency of the more intense types of phaeomelanin. For this reason males and females are combined for graphical representation. *Pinosus* owes much of its brilliance to a more prevalent unmasking of the phaeomelanins by the eumelanins than occurs in *thurberi,* so that the type *p* phaeomelanin shows to full advantage. Stages in reduction of eumelanin are *c, d, dd,* and *y* as in *thurberi.* Type *dd* is slightly less distinctly spotted than in *thurberi,* the areas with and without eumelanin being less sharply contrasted. Microscopic examination of the *y* type reveals essentially no eumelanin. The slight sexual difference in eumelanin in other Oregon juncos holds true in this race. The sexual difference in eumelanin is indirectly the cause of the ruddier appearance of females.

Enough variation in eumelanin of the back is found in *pinosus* to make feasible the calculation of correlation with head color. The coefficient is .274 ± .08. This is decidedly lower than in *montanus,* but it doubtless represents a similar relation of the pigments of the head and back.

Side color varies but little. The few individuals with *thurberi*-like sides do not have other characters of that race.

Variations in tail patterns are shown in the table on page 279. In *pinosus* new types of variants (compared with *thurberi*) are: mixed inner webs of the fifth rectrix, black and partly black outer webs of the fifth, and sixth rectrices with traces of black. Variants that disappear in *pinosus* are: inner web of fourth pure white or nearly white, and third rectrix with trace of white. The variants that occur have average values similar to those for *oreganus*. Average differences between *pinosus* and *thurberi* involve all vanes of the outer four rectrices, and in magnitude they are as great as those between *oreganus* and its neighboring races. The differentiation of *pinosus* and coastal *thurberi* is not quite so great as that of *pinosus* and the interior group, because the coastal birds retain some of the low values for tail white of *thurberi–shufeldti* intermediates. The values for north-coast birds are not the result of *pinosus* influence, for the Mendocino and Sonoma county populations nearest *pinosus* have the greatest amount of white. *Pinosus* controverts the rule of increase in white in tail correlative with paling of the head.

TABLE 25

MEASUREMENTS OF J. O. PINOSUS

Measurement	Sex	No. of specimens	Mean with prob. error	Standard deviation	Coeff. of var.
Wing..............	♂	62	72.05 ± .13	1.50	2.09
	♀	40	69.20 ± .22	2.03	2.93
Tail...............	♂	62	64.03 ± .19	2.27	3.55
	♀	41	61 26 ± .33	2.15	3.50
Bill................	♂	58	8.13 ± .03	.29	3.68
	♀	36	8.07 ± .03	.29	3.66
Bill depth..........	♂	58	5 67 ± .02	.27	4.88
	♀	32	5.76 ± .03	.25	4.42
Tarsus.............	♂	67	19.76 ± .05	.55	2.79
	♀	41	19.62 ± .07	.62	3.18
Middle toe.........	♂	64	11.41 ± .03	.48	4.23
	♀	41	11.27 ± .05	.43	3.91
Hind toe...........	♂	67	7.99 ± .03	.39	4.84
	♀	39	7.83 ± .04	.37	4.74

Indices of variability do not differ importantly from those of *thurberi* except for that of the tail, which is much more variable. The coefficient of correlation of wing and tail is .534 ± .061, somewhat lower than in related races. Other correlations are uncertain; that of tarsus and hind toe, .301 ± .075, possibly has significance. Difference in wing and tail is 11 per cent. Sexual dimorphism of wing and tail is only 4 per cent instead of the customary 5 or 6 per cent, and it is uncertain in other measurements. In general the measurements show less sexual difference than in related races. This is in keeping with a similar situation with respect to head color.

Available weights of breeding males of typical populations number only 17. The average, 17.44 gr., is about 2 per cent less than in coastal *thurberi*. Wing and tail are about 4 per cent shorter than in this division of *thurberi*. The reduction in the planing surface of the wing and tail that supports the weight is therefore disproportionately great.

Color variants such as white-spotted wing coverts have not been found. The usual variation in overcasting in retarded plumages is found. Heavily overcast heads are especially common in females in association with their general light pigmentation. The whole race in a broad sense is one characterized by retarded plumage and low sexual dimorphism. Wearing of the back results in brilliantly colored breeding birds, the brightening effect being comparable to that in *Junco caniceps.* Some of the populations in more arid situations show greater fading than those occupying the fog belt. The sides become more yellowish in the breeding season, but are always prominently colored.

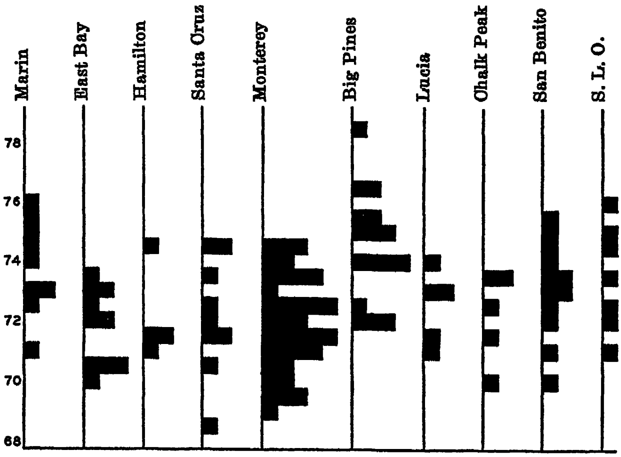

Fig. 22. Occurrence of wing variants in males in populations of *J. o. pinosus* and groups intergradient toward *J. o. thurberi.* Note especially the Big Pines colony.

Geographical variation within the race.—There is little variation locally in the relatively small range of this form that is not a part of peripheral intergradation. The graphs showing intergradation indicate the uniformity within the confines of the race. The various characters show their extreme development at different places, but most often in the Santa Cruz and Monterey districts.

One population displays a most suggestive colonial differentiation. This group is found in the yellow pine and black oak forests of the Monterey Mountains (Big Pines) between the Carmel and Little Sur rivers. The area lies at an elevation of 2700 to 3700 feet, above the fog belt and inland 5 to 9 miles. At lower elevations are large tracts of chaparral that isolate this region from breeding areas in the coastal redwood canyons and lower oak belt. These birds (16 males and 10 females) are distinctly longer winged (see fig. 22) and longer tailed. The females bear out the differences revealed in the males so that there is little doubt that the character of this colony is accurately indicated by the sample. The weights of these birds also are greater, but no features of color are different. The bill averages appreciably longer. Specimens from the coastal canyons a few miles west are small throughout.

One might suppose that this population represented an interior phase of *pinosus,* or in fact a weak race in itself, isolated altitudinally and faunally from the coastal groups, were it not for the fact that samples from the Santa Lucia Mountains to the south do not show like tendencies. Santa Lucia Peak is higher and as much isolated from the coast as the more northern pine areas occupied by the group in question. Across the Salinas Valley to the eastward in the arid mountains about San Benito the juncos are not as distinctly large.

It must be concluded that this population at the headwaters of the Little Sur is differentiated independently of other adjacent populations that occupy comparable habitats. Its isolation is effected by unfavorable tracts of Upper Sonoran chaparral and perhaps by some discontinuity of habitat along the crest of the mountains to the south. The birds may not descend from this region in winter. When one encounters trenchant differentiation in the middle of the range of a race, with only moderately extensive uninhabitable tracts isolating it, his imagination is aroused with respect to the possibility of race formation. This colony could, given the opportunities of continued isolation and at the same time expansion of range, readily lead to a distinct race. Here are the seeds of a race.

Of what does this potential race really consist? The characters concerned presumably are determined by multiple factors. The distribution of sizes shown in figure 22 indicates strikingly the long-winged variants and the absence of short-winged variants that are normal in *pinosus*. But in the females, besides long-winged variants, one small bird, far below the average of *pinosus* females, occurs. Probably occasional small males also occur, but they are not represented in the sample. It is likely, then, that the complex of multiple factors has had a new factor or factors for large size added to it that have spread extensively in the population. If the number of factors concerned is at all large, the variation as a result of this mixture would not in a small sample appear much greater than that of the original racial stock. The occurrence of minimum *pinosus* variants would be extremely rare even if all the *pinosus* factors for small size still were extant in the population.

Distribution.—There are no records of *pinosus* in the fall or winter for localities more than a few miles from the habitats occupied in the breeding season. Definition of breeding areas thus indicates geographic distribution throughout the year. Scattered breeding populations occur in west-central California in the Upper Sonoran and Transition zones from the Golden Gate and Carquinez Straits southward in the hills and mountains of the interior ranges and in coastal wooded areas. The race now breeds in many residential districts of cities in the San Francisco Bay region where formerly it was absent. It breeds occasionally in Contra Costa County (Las Trampas Creek; Mount Diablo), and fairly plentifully in the hills of northwestern Alameda County. There are small numbers in the hills south of Livermore and in the Hamilton Range of Santa Clara County. In San Mateo County, distribution is continuous south along the Santa Cruz Mountains through Santa Cruz County. South of Monterey Bay, *pinosus* breeds in the coastal forests and along the crests of the mountains to the extreme southern part of Monterey County. In San Luis Obispo County intergradation becomes apparent. Isolated colonies occur in San Benito County.

Associations that are inhabited are various and include the following: moist redwood canyons; heavy, but arid, live oak timber (*Quercus agrifolia*); Monterey pine forest consisting chiefly of *Pinus radiata* and *Pinus muricata;* yellow pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga taxifolia*) forests; black oak (*Quercus kelloggii*), golden-cup oak (*Quercus chrysolepis*), and madroño (*Arbutus menziesii*) associations; and digger pine (*Pinus sabiniana*) and Coulter pine (*Pinus coulteri*) forests. Almost any shaded forest land with some form of ground cover that remains green throughout the summer can support nesting birds. Usually, perhaps always, surface water is available. The variation in rainfall and humidity is almost as great as in the range of *thurberi. Pinosus* is tolerant of low zonal conditions to a degree found only in *bairdi.* Accordingly, probably a larger proportion of the race than of *thurberi* exists in regions of low rainfall. Yet a large part of the range of *pinosus* is in the fog belt, an environment met by *thurberi* only on the coast of northern California. Few places in the range of *pinosus* have severe winter climate with significant snowfall, a circumstance which appears to explain absence of migration. In winter, flocks may wander into open country where there is limited cover in the form of isolated clumps of trees. They occur often in orchards in the open valleys. Many are known to stay on the breeding territory in small flocks, possibly family groups.

Relationships with adjacent forms.—*Pinosus* intergrades with *thurberi* in Marin County, and in San Luis Obispo and probably Santa Barbara counties. *Thurberi* at the southern limits of habitable forest along the Russian River in Sonoma County gives little indication of *pinosus* influence. Wing and tail here diminish in average value to begin the downward trend toward *pinosus,* but possibly this is a level characteristic of the immediate coastal regions even farther north. The general decrease in bill depth southward in *thurberi* stops at this point. The colors of head, back, and sides are unchanged. There is, nevertheless, a single male with the *py* type of back; in this one feature the bird is typical of *pinosus.* Tail white actually increases, instead of diminishing toward *pinosus.* Whether there is any mixture of *pinosus* in this group is therefore somewhat doubtful.

In Marin County the situation is different. All characters show intermediate averages, or even attain *pinosus* values. The Marin woodlands are isolated from those of Sonoma County by about 20 miles of country unsuitable for breeding. A similar gap separates the breeding areas north and south of San Francisco Bay. The isolation afforded does not appear great, but in resident populations it means much more than in migratory races. The Marin County representation that has been studied is not as large as might be desired (9 males and 5 females). Averages for wing and tail are about halfway between those of coastal *thurberi* and *pinosus.* The sample is too small to determine whether there is increased variability associated with this intermediate average. In other measurements the margin of differentiation is too small to permit any statement with respect to the average of this group. Tail pattern is in general intermediate (fig. 24). Head color averages as light as in *pinosus,* but, significantly, there is an exceptionally great range of variation for so small a sample (fig. 23). With respect to back, the numbers of *thurberi* and *pinosus* types are about equal. The backs of the group do not show a uniform blend of the two racial types, but can be classified quite as readily into the *t* and *p* categories as can those of members of either race.

The side color of Marin birds is likewise of two distinct types, rarely a blend. *Pinosus* and *thurberi* coloration occurred in about the ratio of 2 to 1. The Marin group, therefore, shows increased variability with respect to characters that clearly segregate as though they might be based on single factors. This variability is not evident in dimensions, probably because of the many factors involved and the limited size of the sample.

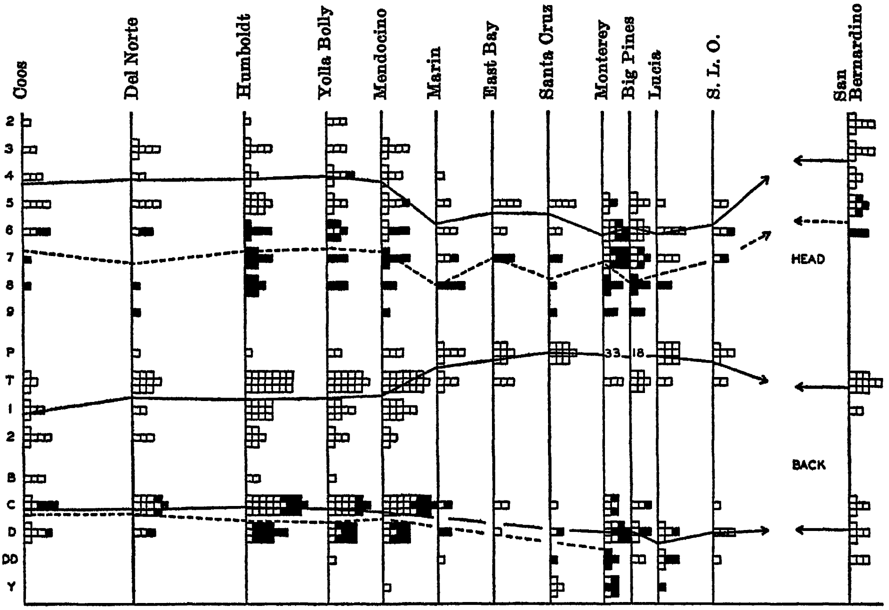

Fig. 23. Geographic variation in head and back color (two pigments) in the immediate vicinity of the coast from Coos County, Oregon (*shufeldti*), south through *J. o. pinosus* to southern California. Connection with group from San Bernardino Mountains (*thurberi*) suggested by arrows through inadequately represented Mount Pinos and San Gabriel Mountain regions. Individuals represented by squares: open squares, males, except upper line for back (phaeomelanin), both males and females; solid squares, females. Samples spaced to scale geographically. For explanation of variants see pages 247 and 284.

The intergradation is like that of *mearnsi* and *montanus* in that all characters become altered in the same region; the zone of intergradation is narrower, however. It appears that the Marin area is inhabited by birds of dual origin and that the group may continue to receive increments from either side. The situation is very different from the intergradation of *thurberi* and *shufeldti,* where modification in the various characters does not correspond geographically and where the intermediates are probably not the result of any immediate racial hybridization.

In San Luis Obispo County occasional pairs of juncos breed among the oaks and digger pines on shaded hill slopes. A group of 7 adults and 3 young from the vicinity of Santa Margarita resemble *pinosus* but show fairly conclusively a trend toward *thurberi*. This is seen in wing and tail length and in tail pattern. In these characters the birds are roughly equal to the Marin County population. With respect to head and back color, the proportion of types is about as in *pinosus*. Two adults, however, have typical *thurberi* sides; the other 5 have *pinosus* coloration. As far as may be surmised, the nature of the intergradation is like that in Marin County, but with a higher percentage of *pinosus* parentage. It is not known how continuous the distribution may be between Santa Margarita and the mountains of southern Monterey County. Because birds successfully breed in the live oak belt, even in such arid interior regions as near La Panza, San Luis Obispo County, it is probable that occasional pairs are scattered throughout the coast range north and south from Santa Margarita. Instead of there being sharply defined barriers as in the northern intergradational zone, in the south there are extremely sparse, scattered populations over a large area. This situation may be as effective a deterrent to intermixture of the main populations of the races as are absolute discontinuities in distribution. Juncos apparently occur in Santa Barbara County (Willett, 1933, p. 174) in a habitat similar to that about Santa Margarita and in scattered forests of yellow pine eastward to Mount Pinos, Ventura County, where typical *thurberi* is present.

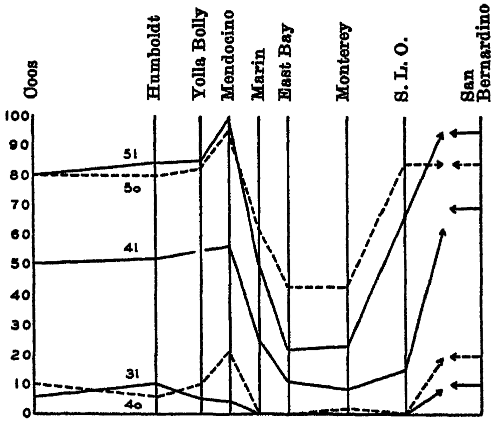

Fig. 24. Geographic variation in amount of white in tail in immediate coastal belt from Coos County, Oregon (*shufeldti*), south through *pinosus* to southern California. Vertical lines represent samples spaced to scale geographically. Figures at left represent percentage of occurrence of variants. *5i* and *5o*, inner and outer webs, respectively, of rectrix 5 pure white; *4i* and *4o*, webs of rectrix 4 mixed rather than black or chiefly black; *3i*, inner web of rectrix 3 with trace of white rather than pure black. Connection with group from San Bernardino Mountains (*thurberi*) suggested by arrows through inadequately represented Mount Pinos and San Gabriel Mountain regions. Males only.

Pinosus, even though tolerant of a considerable variety of environmental conditions in the central coast district, may in its origin have been intimately related to the ancient coastal closed-cone pine forest of this district. The diminution of this forest type since the Pleistocene may have left *pinosus* in areas that now are much more arid than formerly.

Some suggestive points of general resemblance can be found between *Junco insularis* and *pinosus,* the former inhabiting the southern outpost of the coastal closed-coned forest on Guadalupe Island. *Pinosus* of course most resembles *thurberi,* with which it undoubtedly has long been in occasional contact, but its resemblances to *insularis* are nonetheless real.

Pinosus with respect to ruddy coloration and tail markings strongly suggests *J. o. oreganus* and the resemblance may be phyletic. Absence of a ruddy coastal type in northern California is indeed peculiar, since many vertebrate animals show this kind of modification there. Can *pinosus* be a southern residuum of an ancient junco stock somewhat like *J. o. oreganus,* which once crowded southward? It could have been preserved in central California by isolation while lost on the northern California and Oregon coasts where an interior type may have crowded westward. Against this view is the distinct lack of resemblance to *oreganus* in the pale head and the diminution of blackish pigment generally.

Probably the prototypes of the Oregon juncos, which must have had relatively pale heads, early gave rise to ruddier coastal and paler interior types which have since become modified and partly lost, and which remain chiefly in isolated peripheral regions. In final judgment, *pinosus* seems to me to be a remnant of such an early differentiation. It stands in relation to the pale forms, *mearnsi, townsendi,* and *insularis,* as *oreganus* does to *montanus, shufeldti,* and *thurberi.* At the same time it has probably been modified by *oreganus* and *thurberi–shufeldti* contact. If *pinosus* were merely a local coastal differentiate of a *shufeldti–thurberi* stock, why is the head so pale? Southern populations of *thurberi* in arid regions tend to be fully as black as the northern groups. The origin of *pinosus,* as with many other races, seems to have involved not merely adaptation to the present environment, but also historical factors such as interpenetration of races.

Junco oreganus pontilis

This annectent form, which occupies a region between *thurberi* of San Diego County, California, and *townsendi* of the Sierra San Pedro Mártir of Lower California, proves to be relatively uniform in character. Isolation in the Sierra Juárez of extreme northern Lower California is an important factor in maintaining it as a discrete racial entity. Were the region connected by breeding habitat to the north and south, permitting infiltration of related races, the population probably would have taken on the aspects of a hybrid or intergradational complex. *Pontilis* shows a remarkable resemblance to the southern division of *montanus.* But its seemingly independent origin, its geographic range, and its lack of migration, which probably entails other physiologic adjustments to its habitat, preclude grouping it with *montanus.* Such a grouping certainly would obscure the true history of the population.

Racial characters.—*Pontilis* is differentiated from *thurberi* by grayer head (types 5, 6, and 7 in males; 6, 7, and 8 in females). Type 5 in males equivalent ventrally to 5 of *thurberi,* but usually duller on the dorsal surface. Types 6, 7, and 8 of *pontilis* entirely equivalent to similarly designated types of *montanus.* Type 5 of *pontilis* usually grayer above than 5 of *montanus.* Only one male *thurberi* from southern California matches perfectly the heads of the two darkest *pontilis.*

Back of *pontilis* duller brown—olive brown, or nearly drab rather than Verona (fresh), snuff, Sayal, or mikado brown. Back color, classified according to types found in other Oregon juncos, of types 3*c,* 2*c,* 3*d,* and 2*d.* Types 3*c* and 3*d* do not occur in *thurberi,* and 2*c* and 2*d* are found only in the coastal division of this race.

Sides of *pontilis* pinker than in *thurberi,* more nearly vinaceous fawn, hence like the less brown and less yellow variants of *shufeldti* and *montanus.* Color not the cinnamon of *mearnsi* or *insularis.* Contrary to Oberholser's (1919, p. 120) observations, which were based on four birds, I find that the colored area of the sides is slightly more extensive than in *thurberi.*

Tail of *pontilis* with more white on the average on rectrix 3 (30 per cent with some white) and on outer web of rectrix 4. San Diego County *thurberi* equivalent to *pontilis* with respect to rectrix 4, but not 3. Wing 2 per cent longer; tail slightly less than 2 per cent longer, but not significantly longer than in southern California populations; bill, 1½ per cent longer than Tahoe *thurberi,* but equivalent to southern California populations; bill depth about 8 per cent greater; feet similar, but tarsus tending to be longer and hind toe shorter.

For characters differentiating *pontilis* and *townsendi,* see page 303.

Because *pontilis* parallels closely the southern division of *montanus,* it may be useful to summarize such few differences as exist between these two. Color of head, back, and sides in *pontilis* all duplicate common variants in *montanus. Pontilis* more often has white on rectrix 3 (30 per cent as against 1); rectrices 4 and 5 have more white on the average, but same variants present in both. Bill 4 per cent shorter and 2 per cent deeper. In northern *montanus* bill-length similar, but depth even more different; there is of course some difference in head color in northern *montanus.* All these differences are so purely matters of average that there is no feasible means of assorting individuals of the two races.

Nongeographical variation.—A total of 15 breeding males and 7 females has been examined. Additionally, 6 October birds have been studied which almost certainly are *pontilis,* not *montanus.* Six fully grown juveniles also have been used in compiling certain of the average measurements. In such an assemblage the principal color variations in head, back, and sides may be expected to appear. Rare color abnormalities would not be encountered. Average values for tail white and for measurements have high probable errors, yet the main trends probably are indicated.

Head color averages 5.73 in males, varying from 5 to 7, and 6.42 in females, varying from 6 to 8. (For frequency of occurrence of types see fig. 19.)

The range of variation (3) is less than in *thurberi* (4) and the same as in *townsendi*. No greater degree of heterogeneity occurs in this intermediate form, therefore. The reduction of sexual difference to less than 1 is striking; it is equivalent to the situation in *mearnsi*.

Back color is fairly uniform. Phaeomelanin of types 2, 3, and 4 (*townsendi*) occur (see fig. 20). None of these is found in *thurberi* of southern California, but 3 and 4 occur in *townsendi*, although 5 is predominant there. Categories 4 to 6, which represent much reduced phaeomelanin, are not found in more northern members of the rassenkreis. The eumelanin is either of type *c* or *d*. The range of variation is like that in *townsendi* and is less than in *thurberi*, where types *b*, *c*, and *d* occur. Again, no evidence of increased heterogeneity is seen. Oberholser (*op. cit.*, p. 120) commented on the diversity among his four birds and the close approach of some to *thurberi* and of others to *townsendi*, particularly with reference to back and head coloration. It should be emphasized that this diversity does not now appear to be so prominent as suggested by him. The original four birds, it so happens, represent extremes of the race. Sexual dimorphism of the back is comparable to that in *thurberi*, but the scanty evidence suggests that there is also a difference in the phaeomelanin; the females possess on the average more of this pigment as well as less eumelanin. Such a difference is of significance only because a comparable situation is met with in the large series of *townsendi*.

TABLE 26

Average and Extreme Measurements of J. o. pontilis

Measurement	Sex	No. of specimens	Average and extreme measurements
Wing	♂	16	78.48 (75.0-81.2)
	♀	12	73 93 (71.6-76.0)
Tail	♂	16	70.01 (66.6-73.8)
	♀	11	66 58 (61.3-68.7)
Bill	♂	14	7.93 (7.4- 8.6)
	♀	7	7 70 (7.3- 8.2)
Bill depth	♂	14	6.12 (5.8- 6.6)
	♀	7	5.97 (5.8- 6.1)
Tarsus	♂	16	19 91 (19.0-20.5)
	♀	12	19.51 (18.8-20.8)
Middle toe	♂	16	11.24 (10.8-11.8)
	♀	12	11.02 (10.5-11.5)
Hind toe	♂	16	7.87 (7.4- 8.3)
	♀	12	7.64 (7.1- 8.1)

Some variation in side coloration exists, but the state of wear obtaining in the series precludes classification of variants. All but about three or four are visibly more pinkish than average *thurberi*. The width of color area is usually distinctly greater than in *thurberi*, but not, in mass effect, so much greater as is that of *townsendi*. There are a considerable number of *pontilis* that are indistinguishable from certain *thurberi* variants. Nearly all might be confused with certain *townsendi* variants. Doubtless in unworn plumage *pontilis* would prove to be relatively uniform in color, with few *thurberi*-like sides appearing in the population.

The table on page 304 shows the variants in tail pattern present in *pontilis*. Significant new variants, compared to *turberi,* are found in the third rectrix where mixed outer webs appear; we cannot conclude concerning absence of variants of the blacker types in *pontilis,* because the sample is too small. Nevertheless, the addition of white variants and the dropping out of certain black variants in the transition from *thurberi* to *townsendi* is significant.

Indices of variability for *pontilis* cannot be determined, but comparison of range of variation and of histograms indicates no tendency to high variability.

Sexual dimorphism in wing and tail appears to be of the usual magnitude, that is, 5 to 6 per cent. In the other measurements the differences indicated are not to be relied on, but the difference in bill length is like that in *thurberi.* Slight differences in the feet are like those in *townsendi.* Difference in wing and tail is 12 per cent of tail length.

Distribution.—Resident of the Transition Zone forests of the Sierra Juárez, northern Lower California in the vicinity of Laguna Hanson near latitude 30°. Mr. Laurence M. Huey estimates that there is about 20 to 25 miles of scattered Transition Zone forest along this section of the Sierra at elevations between 5000 and 6000 feet. Granitic outcrops are frequent and, in combination with exposure, are causes of the interdigitation of tracts of Upper Sonoran forest. The junco habitat in summer is the parklike yellow pine forest. The fall-taken specimens all come from these mountains. One bird was taken at an elevation of 4200 feet at Los Pozos about 30 miles north of Laguna Hanson, October 31. There is no evidence of migration, therefore. There may be some tendency, as in *townsendi,* to descend to lower levels in winter.

Relationships with adjacent forms.—The spatial separation of breeding ranges of *thurberi* and *pontilis* appears to be about 40 miles. The intervening region, although occupied by the low northward extension of the Sierra Juárez, is not inhabitable in the breeding season. *Thurberi* winters in the range of *pontilis.* To the southward the isolation from breeding areas of *townsendi* is also 40 miles, as far as known, but the distance may be somewhat less. Low passes across the mountains separate the higher zonal areas of the Sierra Juárez and the Sierra San Pedro Mártir.

In the comparisons of *pontilis* with other races and in the analysis of variation within the race, the degree of resemblance to *thurberi* and *townsendi* is set forth in detail. In summary, average coloration of head and back is almost exactly intermediate, but there is a little more overlapping with *townsendi* than with *thurberi.* With respect to these colors, there is little "structural intergradation" or "transgressive variation" with either of the neighboring races. Side color is much as in *townsendi.* Tail white averages close to that in *townsendi,* but there is a distinct indication of intermediacy. The various average measurements are not equally intermediate and they more often are closer to those of *townsendi* than of *thurberi.*

As to the history of *pontilis,* certain possibilities may at least be ruled out. The population is not like the hybrids between *caniceps* and *thurberi,* or like the hybrids between *caniceps* and *J. o. mearnsi.* From these hybrids it differs in being relatively homogeneous, with no greater variability than is found in the adjacent forms It does not contain members that are entirely equal to one or the other of its relatives. If the group has arisen by hybridization, such hybridization does not take place now, nor has it probably occurred in the recent history of the group, for if it had, more diversity would be manifested, even where multiple factors are concerned. If hybridization entered into the origin, certain of the factors of the parents have by now been dropped out of the complex.

Townsendi does not fit well into the scheme of differentiation correlated with environment that prevails in the Sierra San Pedro Mártir. The trend in most local races of vertebrates of that area is toward darker, more leaden hues. In *townsendi* the head is comparatively light and the sides extensively pink, so that one is led to suspect that its characters are not the product of an environmental response to conditions now affecting other animals there. To be sure, the dull color of the back may parallel the modifications in other animals. It is probable that the characters of *townsendi* date back in part to an earlier period of adjustment of the species to environment, and that its present racial characters are more matters of history than adjustments to special conditions now extant. Of course its characters must not be detrimental in its present environment.

Elsewhere I have suggested that *townsendi* and other pale-headed Oregon juncos are peripheral remnants of a lighter-headed, more ancient group of Oregon juncos. Is *pontilis,* then, (1) a remnant of an intermediate stage in the evolution of a darker-headed type, or (2) a result of a fairly old junction of a dark with a light type that has become stabilized and more homogeneous since the time of origin, or (3) an intermediate differentiate, corresponding in some way with the intermediate geographic region it occupies, assuming that these mountain environments affect juncos differently from other vertebrates? I can see no conclusive evidence to support any one of these suppositions, but there is least in favor of the last. Possibly *pontilis* is a direct descendant of a remnant of an ancient intermediate to which there have been additions from time to time by interbreeding with neighboring relatives. It might be thought that *montanus* has established *pontilis* as a remote, separate breeding center through colonization by birds failing to return northward in spring migration. But this seems unlikely on physiologic grounds, and the coincidence of *montanus* colonizing a region where it happened to fit perfectly as a connecting form in a chain of races overtaxes the law of probability.

Junco oreganus townsendi

Townsendi, a strongly characterized race, is the southernmost member of the *oreganus* rassenkreis. It is resident of the Sierra San Pedro Mártir of northern Lower California. Although *pontilis* serves to connect it with the remainder of the rassenkreis, geographic isolation prohibits interbreeding of these two. Even the strikingly differentiated *J. o. mearnsi* interbreeds freely with its neighboring race. *Townsendi* in many respects parallels *mearnsi;* the parallel is not nearly so striking as that between *pontilis* and *montanus,* however.

Racial characters.—*Townsendi* differs from *pontilis* in grayer head; males average 7.6 (7–9), females 8.7 (7–10). Only one male *pontilis* was examined that was as light as type 7. One female *pontilis* was type 7 and one type 8, whereas 1 *townsendi* was type 7 and 5 were type 8, the others being chiefly 9. Head types 9 and 10 in *townsendi* are usually darker dorsally than the same types in *mearnsi,* although equal ventrally. The back of *townsendi* is usually duller, with less phaeomelanin; color hair brown or drab instead of olive brown (*pontilis*); or, of types 3, 4, 5, or 6 instead of 2, 3, and rarely 4. Sides similar, though somewhat more uniformly and extensively vinaceous fawn. White of tail more abundant on the average on rectrix 4 (see table, p. 304). Wing and tail 1 and 2 per cent longer, respectively (the difference cannot be established statistically, but the correspondence of both sexes is confirmatory); tarsus and middle toe about 2 per cent longer.

Townsendi has been compared to *mearnsi,* Dwight having overstressed the similarity by grouping them with *insularis* in a species separate from other Oregon juncos. The important differential characters of these geographically remote races are, briefly: head darker in *townsendi* (average 7.6) than in *mearnsi* (9.5); back duller, usually not with phaeomelanin of type 3 as in *mearnsi;* sides pinkish in both, but *townsendi* not cinnamon and color area narrow. Tail white more or less comparable, but white on the average more extensive in *townsendi,* especially on outer web of rectrix 4 and on rectrix 5. Wing and tail in *townsendi* 2 per cent shorter; bill 3 per cent shorter in males only.

For comparison with *J. insularis,* see page 307.

Nongeographical variation.—The range of variation in head color is shown in figure 19. Not only is the range small, but average deviation from the mean is slight. Sexual dimorphism is slight as in *pontilis* and *mearnsi* and all pale-headed juncos. Back coloration is relatively uniform with respect to eumelanin, especially in males (fig. 20). Sexual dimorphism occurs in phaeomelanin as well as in eumelanin. Side color shows no variations of significant magnitude. Females in fresh plumage appear to average slightly yellower on the sides; this may be related to the dimorphism in comparable pigments of the back.

Because the average occurrence of tail patterns in *pontilis* is not based on a thoroughly adequate series, it is well at this point to note the total alteration that has taken place south of *thurberi.* For this purpose the San Diego County population (34 males) of *thurberi* is used, but it is to be noted that already in this population and in the San Jacinto group an increase in white on rectrix 4 has taken place, compared with Sierra Nevadan *thurberi.* In *townsendi* the following new variants appear: rectrix 3, inner web mixed; outer web with merely a trace of black (mixed type in *pontilis*). A pure black inner web of rectrix 4 fails to appear. A general increase in percentage of occurrence of white types throughout rectrices 3, 4, and 5 is evident. Average sexual difference occurs in rectrices 3, 4, and 5 in *townsendi* as in *thurberi.*

Wing variability is similar to that in *thurberi, shufeldti, pinosus,* and the majority of Oregon juncos, including *mearnsi.* Tail variability is about as great as in *shufeldti* and *mearnsi,* but is higher than in *thurberi* and lower than in *pinosus* and *insularis;* variability of bill and foot is comparable to that in *thurberi* and related races, except that the coefficients for hind toe are especially high. Wing and tail correlation is .741 ± .037. The peculiar wing–

TABLE 27

OCCURRENCE OF TYPES OF TAIL PATTERN IN J. O. PONTILIS AND J. O. TOWNSENDI (IN PERCENTAGES)

	Males		Females	
	pontilis	*townsendi*	*pontilis* (only 11 individuals)	*townsendi*
Rectrix 3				
Inner web:				
trace of white	31	30	18	18
mixed	0	1	0	0
(otherwise pure black)				
Outer web:				
trace of white	6	6	0	0
mixed	6	0	0	0
trace of black	0	3	0	0
(otherwise pure black)				
Rectrix 4				
Inner web:				
pure black	0	0	9	0
trace of white	19	3	36	16
mixed	81	83	55	77
trace of black	0	11	0	6
pure white	0	3	0	0
Outer web:				
pure black	6	0	27	10
trace of white	13	6	0	22
mixed	13	28	45	29
trace of black	31	25	18	18
pure white	38	41	9	20
Rectrix 5				
Inner web:				
mixed	6	0	9	0
trace of black	6	10	55	12
pure white	88	90	36	88
Outer web:				
mixed	0	0	0	2
trace of black	6	3	45	16
pure white	94	97	55	82
Rectrix 6				
pure white throughout				

bill-depth correlation of *mearnsi* is entirely lacking. Foot measurements show the usual indecisive but always positive correlations. The highest is between middle toe and hind toe (.256 ± .074).

Weights of 24 male *townsendi* average 18.83 gr. Sixteen of these are of breeding birds, 9 of fall birds, but the averages for the two groups are insignificantly different. The average weights of *pinosus, thurberi,* and southern *montanus* are 17.44, 17.58, and 17.77, respectively. *Townsendi,* 7 per cent heavier than *thurberi,* would appear to be a larger bird throughout. In other words, the long wing, tail, and tarsus of *townsendi* merely reflect a large-sized bird, whereas they do not in *montanus.* The wing is actually 5 per cent longer in *townsendi* than in *thurberi.* The correlated increase of weight and wing certainly is more to be expected in a sedentary race than in a migratory form like *montanus.*

TABLE 28

MEASUREMENTS OF J. O. TOWNSENDI

Measurement	Sex	No. of specimens	Mean with prob. error	Standard deviation	Coeff. of var.
Wing	♂	70	79.31 ± .17	2.16	2.72
	♀	55	74.68 ± .16	1.81	2.42
Tail	♂	66	71.20 ± .20	2.43	3.38
	♀	52	67.90 ± .18	1.95	2.87
Bill	♂	70	7.94 ± .03	0.34	4.21
	♀	52	7.95 ± .03	0.31	3.88
Bill depth	♂	57	6.07 ± .02	0.25	4.20
	♀	47	6.08 ± .03	0.30	4.95
Tarsus	♂	70	20.10 ± .05	0.63	3.16
	♀	55	19.87 ± .05	0.58	2.94
Middle toe	♂	70	11.49 ± .03	0.39	3.40
	♀	52	11.23 ± .03	0.35	3.14
Hind toe	♂	70	7.90 ± .04	0.44	5.57
	♀	53	7.87 ± .05	0.54	6.95

The wing is 10 to 11 per cent longer than the tail, hence slightly shorter relatively (or the tail longer) than in *thurberi.* This reduction in difference of wing and tail length parallels the reduction in *J. c. caniceps, J. c. dorsalis,* and *J. p. palliatus,* groups in which, in the Rocky Mountain area at similar latitudes, migratory habit disappears.

Sexual dimorphism in wing and tail is 5 to 6 per cent. The bill is identical in the sexes. Tarsus differs by 1 per cent, which is not significant, and the middle toe by 2½ per cent. The dimorphism is thus slightly different from that in *thurberi,* but there is no general reduction in dimorphism to parallel the situation in head coloration.

No instances of white wing spots have been noted. Other aberrations are limited: one spotted albino has been recorded which had a small number of white feathers about the head. *Townsendi* has no retarded plumage marked by overcast neck and pileum. This seems to disappear with reduced head pigmentation much as in some other pale-headed forms. The color of the back is not so much altered by wearing and fading as in *thurberi,* as there are no bright, lightly pigmented regions in the feather vanes to be exposed or to be broken down. The side patches become reduced with wear and often become brighter; they are never abraded to the inconspicuous state common in worn *thurberi.*

Distribution.—Permanent resident of the Sierra San Pedro Mártir of northern Lower California from about latitude 30° 36′ to 31° 10′ (fig. 7). The birds breed in the Transition and Canadian zone forests above 6000 feet, but may descend the mountains to some extent in winter, as at Valladares (2700 feet). Huey (1931, p. 128) records one bird taken October 29, 1930, at San Agustín, at latitude 30°, south of the Sierra [specimen atypical, the back being ruddier than in *townsendi; montanus?*]. The Transition yellow pine forest (*Pinus ponderosa*) is relatively open and arid and is interrupted by granitic outcrops. Ground vegetation is sparse. The juncos are probably concentrated in the parks and grassy basins. In the higher parts of the range are Jeffrey pines (*Pinus ponderosa* var. *jeffreyi*), lodgepole pines (*Pinus contorta*), and small tracts of aspens (*Populus tremuloides*). These forest types doubtless provide favorable breeding areas. On the whole, the mountains do not appear to differ greatly from some of the junco-inhabited ranges of southern California. They are perhaps slightly more arid and the forests more open, but no data are available with which to make a meteorological comparison.

Relationships with other juncos.—In the accounts of *pontilis* and *insularis* the isolation and relationships of *townsendi* are outlined. In these discussions the close relationship with *mearnsi* suggested by Dwight is criticized. The nature of its environment in the Sierra San Pedro Mártir does not suggest reasons for the considerable differentiation of *townsendi* from California forms, nor is the differentiation closely parallel to the alterations in other animals in this area. The racial characters may represent an earlier adjustment to environment, and hence are now probably largely "historical" or paleotelic; the characters may never have been developed in response to a local climatic regime. *Townsendi,* with the other light-headed members of the *oreganus* artenkreis, appears to be a relic of an early *oreganus* stock. In this sense it is related to *mearnsi,* but at present it maintains, or retains, connection with the black-headed races by overlapping of characters.

Junco insularis

Guadalupe Junco

This species, the only truly insular form in the genus, is confined to Guadalupe Island off the coast of Lower California. It possesses nearly all the characters of the rassenkreis *oreganus,* briefly summarized as follows: phaeomelanin on sides, the area sharply demarked from gray of hood; hood convex; both eumelanin and phaeomelanin in back, making this area contrast distinctly with head; iris brown; moniliform pigment in side feathers; some segregation of eumelanin and phaeomelanin pigments in barbules of back feathers. These similarities strongly indicate affinities with the Oregon juncos, but there also exist peculiarities of bill, dimensions, tail pattern, and combinations of colors that strongly differentiate *insularis* from *Junco oreganus*. The relationships with *J. oreganus* are comparable in many ways to the relationships of *bairdi* to the yellow-eyed juncos of the mainland. *Insularis* and the *oreganus* rassenkreis *J. oreganus* may be thought of as the *oreganus* artenkreis.

Principal characters of the species.—Iris brown; lower mandible dull flesh color, parts of maxilla similar, but other areas, especially basally, horn color (maxilla not uniformly horn color as in *bairdi*, though basally it is as dark). Feet dusky flesh color (dried specimens), definitely darker on the average than in other juncos, and never yellowish. Back bister, warm sepia, or (worn plumage) sepia, confluent with similar colors on the wing coverts; back fairly sharply demarked from gray of head. Head brownish gray above, equivalent to type 9 of *montanus–mearnsi* series; chin and throat distinctly lighter than dorsal and auricular areas, contrasting somewhat as in *J. phaeonotus* but tones of gray darker throughout; lores and ocular region blackish as in *J. caniceps;* ventral portion of hood gray, type 11; posterior hood margin distinctly convex. Sides with fairly broad area of pinkish cinnamon, closely similar to *J. o. mearnsi*, but also like the less yellowish variants of *J. o. pinosus.* Tail with two, often three, feathers with some white. Pattern shows less contrast on different rectrices than in other juncos. Pure white outer tail feathers uncommon. Wing and tail extremely short relative to feet and bill; measurements for feet moderately high compared with Oregon juncos. Bill deep and exceptionally long, longer than in *aikeni*, the latter a species obviously much larger throughout. Bill the longest in the genus except for *vulcani;* shape more like the average junco bill than is that of *vulcani;* ratio of bill length to depth equivalent to that in certain races of *J. oreganus*, such as *pinosus* and *thurberi.*

Sexual dimorphism in coloration is essentially lacking. The dorsal surface of the head is a little more frequently mixed with brown in females than in males; the dimorphism is less than in *J. o. mearnsi* and *J. c. caniceps.* Wing and tail show a 5-per cent average difference. Difference in bill length, 1½; bill depth, 3; hind toe, 2 (these latter three differences are barely significant statistically, and others involving the foot are even smaller). Average difference in tail white is found in the outer three tail feathers, especially where there is considerable latitude of individual variation; it is most pronounced on the outer web of the fifth rectrix and on the sixth.

Wear and fading makes the color of the sides more yellowish and brighter. The head changes but little with the season. The back becomes somewhat lighter, but there is no brightening of the brown.

Differential characters.—*Insularis* differs from *J. o. townsendi*, its closest neighbor, in the sepia or bister, instead of hair brown or drab of the back, and in the less pure gray head with black mask; the hood is less contrasted with belly and sides. Sides pinkish cinnamon instead of near light vinaceous-cinnamon to vinaceous-fawn. Wing 12 per cent shorter (not longer than 73 mm. in males, 69 in females; *townsendi* longer than 74 and 72); tail 13 per cent shorter; bill 16 per cent longer (not shorter than 8.5 mm. in *insularis;* not longer than 8.5 in *townsendi*); bill depth 5 to 8 per cent greater; hind toe 5 to 6 per cent longer. White on tail averages less on rectrices 4, 5, and 6. Fifth rectrix rarely without black areas, whereas in *townsendi* usually pure white. Maxilla partly dusky.

Insularis differs from *pinosus* in head and back color, and somewhat in side color. The contrasts are as great as between *insularis* and *townsendi* but different in detail with respect to back, *pinosus* being ruddier than *insularis*. Wing of *insularis* 4 per cent shorter; tail 2 to 3 per cent shorter; bill 14 per cent longer; bill 11 to 16 per cent deeper; tarsus 2 per cent longer; hind toe 7 per cent longer. Total amount of white in tail similar, but *insularis* with less white on outer webs and on outer tail feathers, *pinosus* the converse. Maxilla partly dusky.

Insularis differs from *bairdi* in many of the fundamental points which distinguish the black-eyed and yellow-eyed groups of juncos. Briefly the important differences are: presence (in *insularis*) of eumelanin in back and sides; flesh-colored instead of yellowish lower mandible; eye color brown; convex hood mark; back sepia instead of cinnamon brown and not confluent with color of rump. Wing and tail of both species are small and feet are of comparable size; these are probably parallelisms and perhaps are related to comparable degrees of insularity. The bill of *insularis* is much longer (12 per cent) and more slender than that of *bairdi*. Tail patterns differ in details, though total amount of white similar. Outer webs of *insularis* average blacker and inner webs, especially of inner rectrices, whiter.

Variation.—Coloration is relatively uniform except for the back, which is appreciably ruddier in some individuals than in others; the range is represented by the colors sepia and warm sepia. There is nothing comparable to the retarded and advanced plumage types of the darker-headed races of Oregon juncos. No instances of white wing bars or other comparable plumage abnormalities have been noted.

Variations in tail white are here compared with *J. o. pinosus,* as the latter is as close as any Oregon junco to *insularis* in these respects and may have a special affinity with this form not shared by other members of the rassenkreis (see p. 298). The peculiar tendency toward relatively dark outer webs and reduced contrast between rectrices 4, 5, and 6 is as important a departure from the usual condition in the genus as are great increases or decreases in total amount of white (*aikeni,* for example). Interestingly, *bairdi* shows a disproportionate increase in white on the outer webs compared with its continental relatives. In both, a fundamental change in the factors for tail pattern is indicated.

Wing and tail variability is similar to that in *pinosus,* both races having a fairly high tail coefficient that is not equaled in *thurberi* and *townsendi*. Bill length variation is a little higher than in *pinosus,* but it is equaled in *thurberi;* bill depth and foot measurements are similar. The variation in dimensions reflects no tendency to uniformity such as might be expected as a result of inbreeding in a small insular population; coloration, however, is comparatively uniform.

The coefficient of correlation of wing and tail is .571 ± .049; of tarsus and middle toe, .459 ± .047. The peculiarly long hind toe is not well correlated with the tarsus. A correlation of .261 ± .066 for bill and bill depth may have significance. It is associated with a general increase in the bill, in which a ratio of depth to length equal to that in *pinosus* and *thurberi* is maintained. The factors for bill size that are in part the cause of the greater dimensions may be common factors, thus giving rise to this correlation.

TABLE 29

OCCURRENCE OF RECTRIX PATTERN IN J. INSULARIS AND J. O. PINOSUS (IN PERCENTAGES)

	Males		Females	
	insularis	*pinosus*	*insularis*	*pinosus*
Rectrix 4				
Inner web:				
pure black	3	43	14	54
trace of white	32	49	50	43
mixed	66	0	36	3
Outer web:				
pure black	90	72	95	95
trace of white	8	18	5	0
mixed	2	7	0	5
trace of black	0	2	0	0
pure white	0	2	0	0
Rectrix 5				
Inner web:				
trace of white	2	0	0	0
mixed	40	36	68	54
trace of black	45	38	27	35
pure white	13	26	5	11
Outer web:				
pure black	20	3	68	8
trace of white	21	8	18	16
mixed	49	26	14	43
trace of black	10	18	0	14
pure white	1	14	0	19
Rectrix 6				
Inner web:				
mixed	1	0	5	0
trace of black	29	5	50	14
pure white	70	95	45	86
Outer web:				
trace of white	3	0	0	0
mixed	20	0	23	0
trace of black	45	5	73	14
pure white	32	95	4	86

Distribution.—*J. insularis* occurs only on Guadalupe Island, Lower California, Mexico. The exact distribution on the island is not fully known. I am only acquainted with records from the northern part of the island; because the southern section is barren and arid, it is unlikely that juncos regularly occur there. At the northern end the species occurred originally chiefly in the pines (*Pinus radiata*) and cypresses (*Cupressus guadalupensis*) at elevations of from 3000 to 4500 feet. But Bryant (1887, p. 300) reported it in the palms (*Erythea edulis*) and oaks at lower elevations. In spite of reduction of the forests, the junco has persisted. Even in the earliest report, Ridgway (1876, p. 188) stated that birds came on board ship for food, thus indicating that they inhabited the island at points near sea level. Several exploring parties have found them nesting along the beach, and Swarth (1933, p. 40) speaks of the abundance of juncos at the northeast cove, where young barely able to fly were found. He says: "At the time of our visit [March 16, 1932] the ground was covered thickly with green grass and clovers. The juncos were in the grass or skulking under huge boulders, like Rock Wrens." Thus there is tolerance for a wide range of biotic conditions, fostered by an absence of predators (except the introduced cats) and absence of competitors in the unusual habitats invaded by this species. The breeding of *insularis* in rocky cliffs, grasslands, and beaches devoid of trees is a remarkable departure from the norm for the genus.

TABLE 30

MEASUREMENTS OF J. INSULARIS

Measurement	Sex	No. of specimens	Mean with prob. error	Standard deviation	Coeff. of var.
Wing	♂	84	69.30 ± .12	1.70	2.45
	♀	25	65.70 ± .24	1.82	2.77
Tail	♂	85	62.65 ± .17	2 34	3.73
	♀	22	59.27 ± .30	2.09	3.52
Bill	♂	94	9.30 ± .03	0.37	4.01
	♀	28	9.15 ± .05	0.42	4.62
Bill depth	♂	95	6.59 ± .02	0.31	4.77
	♀	29	6 39 ± .04	0.28	4.49
Tarsus	♂	98	20 20 ± .04	0.62	3.08
	♀	29	20.06 ± .07	0.60	2.97
Middle toe	♂	96	11.54 ± .03	0.42	3.61
	♀	28	11.43 ± .06	0.46	4.04
Hind toe	♂	98	8.55 ± .03	0.40	4.73
	♀	30	8.38 ± .04	0.45	5.38

The lower parts of the island are classed as Upper Sonoran Zone and the forests as Transition. Nelson (1921, p. 94) says: "Guadalupe has the same wet and dry seasons as the California coast. Owing to its situation in the midst of cool ocean currents and the prevalence of the northwesterly winds, it is much cooler than any part of the coast of Lower California at the same altitudes.... Dense fogs are more abundant in winter but prevail also about higher parts of the island throughout most of the year.... During May and June, 1906, W. W. Brown... found the temperature so low that it was necessary to keep a roaring fire in camp.... For 10 days at a time the sun was hidden and everything was... saturated with moisture..."

The climate and the affinity of the flora to that of the closed-cone pine forest of the coast of California point to considerable similarity of the island habitat to that of *pinosus* in the Monterey district of central California. The ability to breed in localities zonally lower than the Transition is common to these two forms, though more pronounced in *insularis*. In this connection the parallel adjustment to Upper Sonoran conditions in the well-isolated *bairdi* is noteworthy (see p. 225).

Relationships with other Juncos.—Guadalupe Island is about 200 miles from the range of *J. o. townsendi* in the Sierra San Pedro Mártir of Lower California. It is more than twice that far from the range of *bairdi* in the Cape district (fig. 7). The range of *pinosus* is 500 miles to the north.

There is no evidence of interbreeding of *insularis* with other juncos today as the result of vagrants crossing the water. Guadalupe is a volcanic island and the intervening depths between the island and the mainland are as great as 2000 fathoms. There is general unanimity of opinion from studies of the biota and geology that the island was never connected with the mainland. Grinnell (1928, p. 10) says that "all of its land birds must have reached it as vagrants, the eight differentiates in more or less remote times. . . . Despite its location 135 miles from the nearest mainland, Guadalupe Island . . . is receiving from year to year vagrant delegates from a wide range of mainland species. Only now and then do the ecologic conditions there, in coincidence with sufficient numbers of arriving vagrants of a given species, plus other critical factors of persistence, permit of colonial establishment." This is a very satisfactory statement relating to the mode of origin of *insularis*.

There is a record of Bryant's (1887, p. 299) of another form of junco on the island. The bird, which was collected, was reported as *J. o. oreganus,* but it could have been one of several races of the *oreganus* group; the specimen probably was destroyed in the San Francisco fire of 1906. Bryant remarks that the bird was attacked by the local juncos. Possibly this action meant no more than that local birds were beginning to breed (February 16), for most juncos are extremely tolerant of related species in winter. Even though juncos can cross to the island today, *insularis* as it exists now, with reduced wings (see Lucas, 1891, p. 220), would probably not be able to fly to the mainland.

The source of the ancestral vagrant that established *insularis* remains an open question. There is nothing favoring an idea of origin from the south. The resemblances of *insularis* are with the *oreganus* rassenkreis; furthermore, southern juncos are relatively sedentary. The most likely ancestor would be a boreal form which, at least in the past, was to some degree migratory.

Ridgway was struck by the resemblance of *insularis* and *mearnsi* (*annectens* of Ridgway, 1877, pp. 60–64). This was occasioned by the similarity of their gray heads and pink sides. At the time of his writing, the pale-headed *pinosus* was not known and *mearnsi* was thought of as more distinct from *J. oreganus* than has since proved true. There is a remarkably close approach of the head color of female *pinosus* to *insularis*. Dwight (1918) pursued the idea of relationship of *mearnsi* and *insularis* further, even placing them in the same species. This again was done because of similar head color and pinkish tones of the sides These colors, in his opinion, are qualitative characters and are indicative of specific unity. Elsewhere I have indicated that gray and black are colors dependent on different quantities of the same eumelanin pigment. The slight distinction between the more ruddy phaeomelanin of the sides of *mearnsi* and the yellow phaeomelanin of other Oregon juncos is not impressive. Indeed, some *insularis* and *pinosus* are not certainly distinguishable in this regard. Wherein, then, are there grounds for stressing "qualitative differences"? The back of *insularis,* rather than being close to *mearnsi,* is the same as that of certain variants in *shufeldti* and *montanus.* Dwight's concept of *mearnsi* (or *insularis*) as a dispersed species consisting of the races *mearnsi, townsendi,* and *insularis* was destroyed by the discovery of an intermediate form *pontilis,* which links *townsendi* with *thurberi.* Thus *townsendi* with its "qualitatively different" pink sides is associated with yellow-sided races of the *oreganus* rassenkreis.

Despite the overstress on similarities of *mearnsi* and *insularis,* a certain fundamental, rather remote, relation still is to be conceded. Around the southern, eastern, and western periphery of the *oreganus* artenkreis are more or less isolated, light-headed forms with richly colored sides. These are *mearnsi, pinosus, townsendi,* and *insularis* (see discussion, p. 298). In all, the sexual dimorphism is relatively low. It is likely that these forms are to some degree relics of an original *oreganus*-like stock. Their paleness far surpasses that which might be expected to appear in association with the aridity of their environments. Perhaps the fully black-headed junco is a newer type, bearing the same general pattern of its paler relations, which has originated in and come to dominate the center of the area of the artenkreis, and which has carried sexual differentiation to greater extremes.

Accordingly, *insularis* may date back to an early period in the evolution of the *oreganus* group, quite possibly retaining in its isolation much of the ancestral coloration. The other relics have had comparable histories, but each has been subject to different influences and to the intermixing of new stocks (especially *pinosus* and *townsendi*). Peculiar tail pattern, short wing and tail, large bill, and moderately large feet are specializations developed in *insularis* and, except the first, are features often associated with insularity. Comparable trends are seen in lesser degree in *pinosus* and *bairdi.* The most primitive features of *insularis,* which may even hark back to a period of closer approach of *oreganus* to *caniceps* and *phaeonotus,* are the black loral area and the dusky maxilla.

Primitive *oreganus* migrants from the range of the rassenkreis to the north may have established *insularis.* Considering present migration routes and similarity of forest habitat, we may suppose that these vagrants probably came from the coast of California, where *pinosus* now breeds, rather than from the Rocky Mountain district. In the Pleistocene, the Monterey coastal forest was a larger and more southerly extensive biotic area which may have brought the ancestral stock into the San Diegan district or to the islands of southern California. However, establishment of *insularis* may have been pre-Pleistocene.

Rassenkreis **Junco hyemalis**

Slate-colored Junco

This rassenkreis is small in point of numbers of forms, but it occupies an area greater than that of any other rassenkreis. The central and principal race, *hyemalis*, ranges from the northern coast of Alaska to the Atlantic seaboard. The race *carolinensis* is a differentiate in the southern Appalachian Mountains. Another form, not obviously a local differentiate, and probably a stabilized hybrid, is found in the Cassiar district of British Columbia. The *hyemalis* rassenkreis is the most boreal one of the genus; it extends north to the limit of trees and reaches such latitudes as 71° at Point Barrow, Alaska. The southern limits coincide roughly with the occurrence of Oregon juncos in southern coastal Alaska, in coastal British Columbia, and in central interior British Columbia. In the interior of the continent the plains regions limit the breeding area in the south.

Junco aikeni, a conspicuously differentiated, isolated species, obviously is related to this rassenkreis and is geographically complementary to it. With *Junco hyemalis* it may be said to constitute an artenkreis of *hyemalis*-like juncos. Except for *carolinensis,* members of this artenkreis migrate, often to great distances south of the breeding area. The movements of *carolinensis* in winter appear to be chiefly altitudinal.

Principal characters of the rassenkreis.—Sides with some feathers, if not all, fairly pure gray or slate (eumelanin pigment). Slate may be obscured by extensive buff or cinnamon, but, even so, it is visible beneath tips, at least far anteriorly. Ventral hood margin concave posteriorly, owing to confluency of gray of breast and sides. Lores and ocular region not distinctly darker than remainder of head. Back area indistinctly or not at all differentiated from dorsal surface of head. Back chiefly gray or slate, never deep black; phaeomelanin, if present, uniformly distributed on dorsum. Phaeomelanin occurs chiefly on distal parts of feathers and never produces a bright or ruddy brown. Eumelanin is uniformly distributed in barbules, except at extreme bases. When phaeomelanin is present, it is not restricted to clear basal parts of barbules, as it usually is in *Junco oreganus,* but is suffused throughout as though eumelanin were partly altered. Thus, in the arrangement of pigments there is some resemblance to *Junco alticola,* except that in *hyemalis* eumelanin predominates. Pigments of sides, when other than black or gray, also show mixture in barbules, but there is some tendency to concentration of eumelanin distally. Phaeomelanin or eumelanin is less distinctly moniliform than in *Junco oreganus*. Phaeomelanins appear chiefly in distal parts of vanes in feathers of sides.

Iris dark brown; bill and feet flesh color. Tail with two outer feathers chiefly white; usually some white on fourth rectrix. Size moderately large.

Junco hyemalis hyemalis

This race is associated with the transcontinental boreal forests. Except in certain populations in the southeast which are intermediate toward *carolinensis,* migration is extensive and is participated in by all individuals. In view of the size of the breeding range, the degree of geographic differentiation within it is exceptionally slight, much less than within the relatively small areas occupied by *J. o. thurberi* or *J. o. shufeldti*. However, significant discontinuities in distribution north of central New York are lacking and the environment is comparatively uniform in the summer season. The areas of intergradation between *J. h. hyemalis* and the other two members of the rassenkreis are extensive.

An exceedingly great amount of individual variation is characteristic; the prevailing slaty pigmentation is strongly modified or replaced by buffs and browns (phaeomelanins) to produce striking retarded plumages of varying degrees. Such plumages are not entirely matters of sex or immaturity, and so they cannot properly be named as such The retarded plumages are comparable to those in *Junco oreganus,* but they affect more areas of the body and lead to greater diversity in appearance They involve suffusion of the entire plumage and not so much just the feather tips.

Differential characters.—Features of *hyemalis* that distinguish it from *Junco oreganus oreganus, J. o. montanus,* and *J. o. mearnsi* are, most importantly, those already given as characteristic of the rassenkreis *hyemalis:* gray of varying degree in the sides which precludes appearance of uniformly colored buff, brown, or pinkish cinnamon sides, as in *Junco oreganus;* ventral hood line never convex posteriorly; head never sharply set off from back.

In addition to noting these fundamental differences, it is well to compare other details with races of *oreganus* which border the range of *hyemalis. J. h. hyemalis* differs from *J. o. oreganus:* back dark mouse gray, or dark olive gray to olive brown instead of Prout's brown, Brussels brown, or raw umber; head slate, not darker than type 6 in males, a type that is rare in *oreganus,* or else head overcast with less brilliant ruddy buff and brown; tail with fifth rectrix much more often pure white; average amount of white on fourth rectrix greater; wing and tail, 4 per cent longer; bill depth, 3 per cent greater; middle toe, 3 per cent shorter.

Contrast in coloration between *hyemalis* and *J. o. montanus* is similar to that between *J. h. hyemalis* and *oreganus*. The head of *hyemalis* is lighter, although the contrast is not so strong as with *oreganus,* especially so far as southern *montanus* is concerned; the back of *hyemalis,* when suffused with brown, may be the same as that of *J. o. montanus,* but basally the feathers are gray or slate, not brown. *Montanus,* even in decidedly retarded plumage, usually shows some trace of head demarcation dorsally. The heads of females in retarded plumage and with similar degrees of buff suffusion are nearly always paler slate in *hyemalis,* but an extremely pale buffy female *montanus* may be no darker slate than a less retarded female *hyemalis*. The tail markings, on the average, are nearly the same. Significant differences in average measurements between northern *montanus* and *hyemalis* are: tail, 1 per cent shorter in *hyemalis;* bill depth, 3 per cent greater (equal to southern *montanus*); tarsus, 1 per cent longer; toes, 2 per cent longer.

Hyemalis differs from *mearnsi* much as it does from *montanus* with respect to sides and back, except that the sides of *mearnsi,* which lack phaeomelanin and are of great extent, are even more strikingly different. The back of *mearnsi* is always slightly lighter brown (nearer drab) and the pileum never more than lightly overcast, the head demarcation being preserved dorsally. Male *hyemalis* are darker headed than *mearnsi,* which latter have head types 9 and 10 instead of 6 or 7 (relatively lighter dorsally). Female *hyemalis* may match male or even female *mearnsi* in general intensity of gray, but the gray is always less pure or ashy in tone because of associated buff tips. *Hyemalis* shows less white in the tail, particularly on the third and fourth rectrices. Average differences in measurements are: wing, 3 per cent shorter; tail, 5 per cent shorter; bill, 2 per cent shorter, bill depth, 3 per cent less; tarsus, 2 per cent longer; hind toe, 3 per cent longer.

For characters differentiating *hyemalis* and *aikeni* see page 346; for *carolinensis,* page 326.

Nongeographical variation —White tips on the wing coverts occur more frequently in *hyemalis* than in any other form except *aikeni* White is never found on the secondaries as in some *aikeni,* but it may be fully as prominent on the secondary coverts. Some pure white areas occur in 2.66 per cent of the 1556 birds that were examined No geographic localization of occurrence is apparent. With so large a sample it is possible to state the relative abundance in the sexes: 3.50 per cent in 970 males, 1.19 per cent in 586 females. The highest occurrence in other juncos, exclusive of *aikeni,* is 1.82 (in *mearnsi* both sexes combined). These occurrences probably represent mutations that have occurred a number of times in different places and have to varying degrees been spread through the population. The different occurrence of the character in different races may be as much a matter of success in spreading as of rate of mutation.

Variations in the suffusion of phaeomelanin in the plumage have been described in the foregoing sections. There is no doubt that this occurs more frequently and more extensively in females than in males, but it is also clear that no complete sexual difference exists. Females probably never attain a pure slate-colored back, but neither do all males. Without large numbers of specimens at hand at one time, it is impossible to classify different stages of retarded plumage and to indicate their occurrence within each sex. Much the same holds true for age. The age of relatively few fall birds has been reliably determined from the skull, but a few have shown conclusively that adult and immatures of the same sex and season may on occasion be identical in coloration. Adult males in fresh plumage always have some buff tipping.

Where buff tipping is prevalent, wear decidedly alters the mass color effect. Wear always tends to purify the gray and slate of the hood and to make it slightly darker, for the bases of the vanes are heavily pigmented. In females that are heavily suffused with phaeomelanin, little alteration may occur by the time of the breeding season. The faintly brownish backs of females usually are accentuated by wear, but do not become sharply defined. Prenuptial molt, as Dwight has stated (1918, p. 287), is not an important factor in these changes.

Head color of males varies with respect to the gray of the dorsal surface of forehead and pileum. Certain of the series of eastern breeding birds were classified as follows: light slate (dorsal surface equals type 8 of *montanus,* relatively lighter ventrally); slate (equals 7 dorsally); dark slate (equals 6 dorsally); dull black (darker than 6 dorsally, but not equal to 5). A certain amount of variation in the proportion of occurrence of these types was found, but only in areas where there is a gradient toward *carolinensis* or where *Junco oreganus* or *J. hyemalis cismontanus* is approached. The percentages of occurrence of types in eastern Canada is: 10 (1), 60 (2), 17 (3), 13 (4). In the Mackenzie-Athabasca area and in Alaska the proportions are similar, with about 50 per cent of type 2. Heads of females, when gray, vary from slate through light slate to still lighter categories equivalent dorsally to types 9 and 10 of *mearnsi.* Females are most frequently light slate, or type 9.

Inner webs of the fourth rectrix with only a trace of black occur rarely in other samples of *J. h. hyemalis* than the one here tabulated. In *carolinensis* there are a few variants with pure white outer webs on the fourth that do not occur in *hyemalis;* and there is none with black on the sixth. No well-represented class of variants is present in *carolinensis* that is not present in *hyemalis.* Sexual dimorphism in *hyemalis* is remarkably slight; only on the inner web of the fifth rectrix is it significant. In *carolinensis* dimorphism is definite on both webs of rectrices 4 and 5.

The chief difference in pattern between the races *carolinensis* and *hyemalis* lies in the greater average amount of white in *carolinensis,* but because of the difference in sexual dimorphism in the two, females of the two are not strongly differentiated. In other words, the sexual dimorphism in *carolinensis,* which is of normal amount, is about equal to the racial difference in males. The racial difference is not great compared with that obtaining between some forms of *Junco oreganus.* Also to be emphasized is the near identity of pattern in *J. h. hyemalis* and *J. o. montanus,* though in other respects they seem fundamentally differentiated.

Coefficients of variability are similar to those in Oregon juncos. There are no significant departures from the values for *J. o. montanus* except in wing length, which is lower, more as in *J. o. oreganus.* The coefficients for *carolinensis* are extremely similar to those of *J. h. hyemalis.* In computing averages for different subgroups within *hyemalis,* coefficients of variability also were determined. These usually depart from the values here tabulated by little more than the rather large probable errors of the coefficients. Wing and tail are much less variable (1.63 and 2.70) in the group from the maritime provinces of the Northeast. Tail also is low in the New England area. Tarsus is exceptionally low (1.80) in Alaska. Differences in coefficients in the other more variable characters are probably not to be trusted. Sexual difference in wing is 6 per cent; tail, 5 per cent; bill depth and middle toe, 2 per cent; tarsus, 1½ per cent; otherwise it is absent. Difference in wing and tail is 12 per cent in males, 10 in females.

Wing and tail are well correlated, as usual: ♂ .676 ± .036. No correlations involving wing and tail with bill or feet occur. Among the foot parts there are the following correlations: tarsus and middle toe, .316 ± .056; tarsus and hind toe, .218 ± .060; middle toe and hind toe .499 ± .048.

Geographical variation within the race.—Attention has been directed to the remarkable uniformity of populations within the extensive range of *hyemalis*. The few minor differences that occur are shown by means of graphs that illustrate the gradients in characters toward *carolinensis*. In measurements, the population breeding in the maritime provinces of Canada is peculiar with respect to the bill, which is long. In New England, wing and tail

TABLE 31

OCCURRENCE OF RECTRIX PATTERN IN J. H. HYEMALIS (QUEBEC) AND J. H. CAROLINENSIS (IN PERCENTAGES)

	Males		Females	
	J. h. hyemalis	*carolinensis*	*J. h. hyemalis*	*carolinensis*
Rectrix 3				
Inner web:				
trace of white.................	2	9	0	0
Outer web:				
trace of white.................	2	1	0	0
Rectrix 4				
Inner web:				
pure black...................	16	1	22	6
trace of white.................	50	22	48	44
mixed.......................	34	71	30	47
trace of black................	0	5	0	3
pure white..................	0	1	0	0
Outer web:				
pure black...................	54	14	48	44
trace of white.................	10	21	26	22
mixed.......................	20	36	13	22
trace of black................	12	15	9	8
pure white..................	4	14	4	3
Rectrix 5				
Inner web:				
mixed.......................	14	1	39	14
trace of black................	18	8	13	33
pure white..................	68	91	48	53
Outer web:				
trace of white.................	0	0	4	3
mixed.......................	36	9	35	22
trace of black................	20	18	13	22
pure white..................	44	73	48	53
Rectrix 6				
Inner web:				
pure white..................	100	100	96	100
Outer web:				
pure white..................	100	100	96	100

diminish to the lowest level for the race despite the fact that this group in certain characters begins to grade toward the large *carolinensis*. The northeastern maritime group again differs in tail white. White on the fourth rectrix is materially greater on the average, approaching the situation in *carolinensis*. The fifth rectrix does not show similar modification. The Alaskan population has some reduction of white.

TABLE 32

MEASUREMENTS OF JUNCO HYEMALIS HYEMALIS

(Groups from Alaska to Quebec north of the St. Lawrence River)

Measurement	Sex	No of specimens	Mean with prob error	Standard deviation	Coeff of var
Wing	♂	104	78.17 ± .12	1.79	2.29
	♀	50	73.50 ± .12	1.32	1.79
Tail	♂	104	68.98 ± .14	2.22	3.22
	♀	48	65.62 ± .20	2.06	3.14
Bill	♂	92	8.02 ± .02	0.34	4.23
	♀	53	8.03 ± .03	0.34	4.20
Bill depth	♂	89	5.98 ± .02	0.27	4.65
	♀	41	5.87 ± .03	0.29	4.89
Tarsus	♂	116	20.56 ± .04	0.65	3.16
	♀	57	20.26 ± .05	0.58	2.85
Middle toe	♂	116	11.65 ± .03	0.53	4.77
	♀	57	11.38 ± .03	0.38	3.34
Hind toe	♂	113	8.29 ± .03	0.38	4.61
	♀	57	8.24 ± .04	0.39	4.82

Distribution in the breeding season.—Generally distributed from the Arctic coast in Alaska southeastward in the transcontinental forest to Labrador, Newfoundland, Nova Scotia, New England, and New York; in the latter two regions intergradation is perceptible.

Alaska.—From vicinity of Point Barrow (Bailey, Brower, and Bishop, 1933, p. 38) and probably other parts of Arctic coast, south to base of Alaska Peninsula, Kenai Peninsula, and Prince William Sound, and from Bering Strait eastward into Yukon. Not known to breed on the Alaska Peninsula or the Aleutian Islands (see fig. 16).

Yukon.—Probably north nearly to Arctic coast. Distributed throughout drainage system of Yukon River south to about 61°, beyond which change in character begins.

Northwest Territories.—North along Mackenzie River probably to delta region, certainly as far as Fort Good Hope. Known from upper Mackenzie Valley, and Great Slave Lake district (fig. 28). Northern limits probably coincide closely with forest margin that runs from mouth of Mackenzie River southeast toward Churchill on Hudson Bay.

British Columbia.—May occur in pure form in northeast corner of province from Fort Nelson northeastward. No specimens examined.

Alberta.—South nearly to Edmonton in central and eastern section. On plains just east of mountains and west of Edmonton intermediate populations occur. In western half of province pure populations probably occur southwesterly at least to Peace River Landing and Lesser Slave Lake.

Saskatchewan.—South to about latitude of Prince Albert, except along eastern boundary, where it follows edge of prairies southward to a point slightly north of Canadian Northern Railway.

Manitoba.—From shores of Hudson Bay south nearly to Winnipeg; east of Winnipeg extends south to Lake of the Woods.

Ontario.—Throughout the province as far south as Toronto, but sparsely and irregularly distributed in vicinity of Lake Ontario and upper St. Lawrence River.

Quebec.—Throughout province north to Richmond Gulf on Hudson Bay; also on Magdalen Islands.

Newfoundland Labrador.—North to Tikkoatokok Bay, but probably not beyond the Kiglapait Mountains just north of there.

Newfoundland and Maritime Provinces of Canada.—Occurs throughout, including Sable Island.

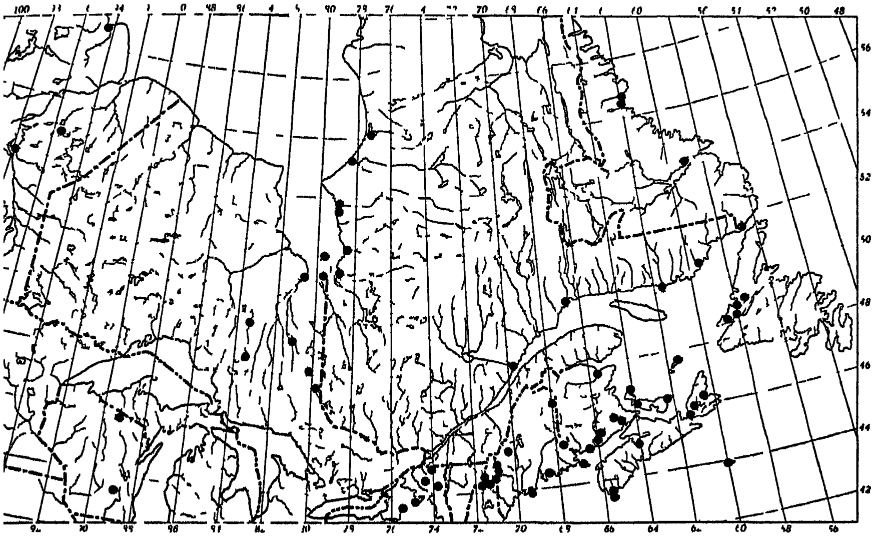

Fig. 25. Distribution of breeding *J. h. hyemalis* in eastern Canada and the northern United States. Each symbol represents a locality from which specimens of this junco have been examined.

Minnesota.—Roberts (1932, p. 406) reports breeding "in the coniferous forests of the northern counties, as far south as central Pine County (Surber) and as far west as Itasca Park and eastern Marshall County. The Junco, as a nesting bird, is confined well within the typical *Canadian Zone,* not reaching the boundaries of this region either on the south or west."

Wisconsin.—Northern half, south to about latitude of Green Bay, Brown County. A bird taken May 25, 1913, at Beaver Dam, Dodge County, may be a late migrant (see Roberts 1932, p. 406, for dates).

Michigan.—Northern peninsula and southern peninsula, south to Saginaw Bay, but also sporadically to Kent and Ingham counties (Barrows, 1912, p. 513).

New England.—Throughout Maine, Vermont, New Hampshire, and Massachusetts, and sporadically in Connecticut, principally in north and west (see Forbush, 1929, p. 86).

New York.—Northern section, especially the Adirondack Mountain area, and Catskill Mountains of southeastern New York. Sporadically in western section from Tompkins County to Cattaraugus County and east of Hudson River from Rensselaer County to Dutchess County.

Birds breeding in Pennsylvania are considered intermediate toward *carolinensis.* This probably is true also for those reported from northeastern Ohio (Campbell, 1940, p. 173).

Any attempt to describe the habitat of *hyemalis* cannot but fail to cover many local situations within the extensive geographic range. Further, information relative to the exact associations in which slate-colored juncos breed is not so plentiful as might be wished. The author has only a limited field acquaintance with this form and must therefore compile information from various sources, credit for which can be given only in part. The chief requirements of *hyemalis* are like those of Oregon juncos. Bush and tree cover is essential, with moist, somewhat open, plant-covered ground in which to forage. These conditions are encountered widely in the northern forests, except where the trees become too dense or the ground too much saturated with water. *Hyemalis* has a fairly high tolerance for dense forests. Grinnell (1900, p. 52) says that in the Kowak River Valley, Alaska, "they were always met with in the deep spruce woods." Places where I have seen the species in Pennsylvania in the broad-leaf forest seemed densely grown to vegetation compared with the habitat of southern races of *J. oreganus*. Probably the habitat of *Junco o. oreganus* is as dense as that of any junco, however. Swarth (1926, p. 132) speaks of the race *"connectens"* (= *J. h. cismontanus*), which undoubtedly is similar in habitat preference and tolerance, "singing from tops of bushes and small trees" in the Carcross region, Yukon. Nests "were all in fairly open bottom land, on the ground, and well concealed in sheltering grass and other vegetation." Thus is indicated a considerable range of tolerance in openness of habitat that seems to hold throughout the range. Broadly speaking, absence of trees is the limiting factor in the north, and prairie or austral forests the limiting features southward except where other species and races replace *hyemalis* in this direction. On the coast of Alaska, the mountains and glaciers between Prince William Sound and Yakutat Bay appear to serve as a barrier between *hyemalis* and *J. o. oreganus*. How complete a barrier they are must be answered by further exploration. In Alaska the more southern mountains may be inhabited up to 3500 feet, but in the north the junco is restricted to the forests of the valleys, the only places, in fact, where forests occur. Precipitation varies from 130 and 190 inches in the Prince William Sound district to only about one-tenth as much in parts of the interior.

Trees which dominate the forests occupied by *hyemalis* are various. In coastal Alaska, Sitka spruce (*Picea sitchensis*), giant cedar (*Thuja*), and alpine hemlock (*Tsuga mertensiana*) are the prevalent conifers. In the interior of Alaska, white spruce (*Picea canadensis*) and black spruce (*Picea mariana*) are the important forest types, together with balsam poplar (*Populus balsamifera*) and aspen (*Populus tremuloides*). These four comprise much of the forest of the interior of the continent, with the addition of larch (*Larix americana*), which becomes more prevalent east of Alaska, balsam fir (*Abies balsamea*), and Banksian pine (*Pinus banksiana*). This forest extends east of Hudson Bay to Labrador. In southern Quebec, Ontario, and the Maritime Provinces, beside the coniferous forests, deciduous forest types constitute in part the habitat of juncos. Some of the trees here concerned are beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula lutea*). White pine (*Pinus strobus*) at lower elevations and red spruce (*Picea rubra*) at higher elevations together with these hardwood forest trees constitute junco habitat in New England and New York.

Distribution in winter (November 1 to March 1).—Winters chiefly south of the breeding range, except in the eastern United States, where certain populations may have only a vertical migration (Forbush, 1929, p. 87). Most of the wintering population is found in the United States east of the Rocky Mountains, south of latitude 45° and north of latitude 33°. West of the Rocky Mountains a great many, perhaps half, of the *hyemalis*-like juncos are *cismontanus* or hybrids with *J. oreganus*, and west of the Cascade–Sierra Nevada system typical *J. h. hyemalis* is exceedingly rare.

The exact limits of known winter occurrence based on specimens examined by me or on records reasonably attributed to *hyemalis* rather than *cismontanus* are as follows: northward as far as southern British Columbia (Fraser and Okanagan valleys), probably northern Idaho, Montana, and North Dakota (no definite records north of southern Idaho, Wyoming, and Nebraska), Minnesota except the extreme north, Wisconsin, the southern peninsula of Michigan, Ontario north at least to Toronto, southern New York north to Oswego and Warren counties, New England north to southern Vermont, New Hampshire, and Maine (*fide* Forbush). Winter specimens from central Maine (Moosehead Lake) and Nova Scotia (no specific locality) have been examined. In the west there is a winter-taken specimen from Juneau, Alaska. A record (Palmen, 1887, p. 284) for eastern Siberia (June 4, 1879) probably represents lost or strayed birds that might, however, have wintered on the Asiatic side. Southward, through California, exclusive of the coastal district of northern California, to about latitude 32° in northern Lower California; southern Arizona, northern Chihuahua (Chihuahua City), Texas to Beeville, the gulf coast of Louisiana, Mississippi, and Florida south to Orange County. There is a record (Howell, 1932, p. 467) from Chokoloskee, Collier County, southern Florida.

Relationships with adjacent forms. Junco h. carolinensis.—Beginning in New England and continuing southwestward, gradation in averages of characters takes place which culminates in a terminal population in the Carolinian mountain region that is fairly well differentiated from *hyemalis* of Canada. No new characters appear, except for certain extremes in size and in amount of white in the tail. The differentiation consists of different average occurrence of variants.

The accompanying tabulation (see p. 322) shows the occurrence, in percentages, of the head types of males along this gradient. The geographic areas there represented are: (1) eastern Canada, including Ontario, Quebec, and the Maritime Provinces; (2) New England, including also the Adirondacks of northern New York; (3) southern New York, the Catskill Mountains south of the Mohawk River; (4) Pennsylvania, all parts of the state where juncos breed, from the Delaware River south, and including western Maryland; (5) North Carolina, chiefly, but including adjacent parts of Tennessee, Georgia, and Virginia north to the latitude of the James River. At least 25 males from each area were used in computing averages, and from Canada and North Carolina the number exceeded 100.

To be noted particularly is the shift of the mode from slate to light slate in passing southward and the disappearance of dark slate and dull black types. At least 10 per cent of the Canadian population cannot be distinguished from those of the southernmost area on the basis of this series of characters. Some of the types occur in all the groups, but, the proportion being different, the patterns of the group mosaics differ accordingly.

The degree of discontinuity between these intergrading populations is variable. The breeding populations of Canada and New England are continuous. The southern New York group from the Catskill Mountains is isolated to some extent. There are regions to the north and east along the Mohawk and Hudson rivers and to the southwest in the Delaware Valley that are not occupied by breeding juncos. The discontinuity between the Catskills and the Berkshire Hills is not more than 30 miles, and that between the Catskills and the mountains of northeastern Pennsylvania is not more than 60 miles. Breeding juncos are distributed fairly continuously in the mountains of Pennsylvania from Luzerne and possibly Lackawanna and Wayne counties in the northeast and Tioga, Potter, McKean, Warren, and Erie counties in the north, south into Maryland. The juncos of western New York are not isolated from those of Pennsylvania; no representations from the former region have been examined. The material from Pennsylvania may be subdivided into a small northeastern group (7 males), northeast of the west branch of the Susquehanna River, a northern group (11), north of latitude 41° and the west branch of the Susquehanna, and a southern group (21), south of the west branch of the Susquehanna (fig. 26). With respect to head color, the three groups seem to form a unit. No higher percentage of light slate heads occurs in the southern group than in the northern and northeastern groups. Breeding range appears to be fairly continuous south through western Maryland and eastern West Virginia. No adequate samples from these states or from Virginia north of the James River have been examined. Probably this area, which connects Pennsylvania and southern Virginia, has a population less extreme in *carolinensis* character than those farther south.

Head type	Eastern Canada	New England	Southern New York	Pennsylvania	North Carolina
Light slate	10	25	55	60	98
Slate	60	50	30	40	2
Dark slate	17	16	15	0	0
Dull black	13	8	0	0	0

The graph (fig. 27) shows the increase in all measurements to the southward. This increase is most pronounced in wing, tail, bill, bill depth, and middle toe. Wing and tail begin to increase south of New England and continue at a nearly uniform rate; the gradient for tail length is steeper, thus establishing a different ratio of wing to tail in *carolinensis*. Averages for both these measurements change within the Pennsylvanian region, as shown when the subgroups (see above) are analyzed, so that the gradient is uniform and unbroken through this sector. The northern Pennsylvania subgroup is intermediate between the northeastern and the southern.

Bill length reaches a low point for *hyemalis* in southern New York. From here south it increases steadily through Pennsylvania. Bill depth is exceptional in that the value typical of *carolinensis* is attained in Pennsylvania. The southern subgroup in Pennsylvania exceeds slightly the average for *carolinensis,* whereas the northern and northeastern subgroups are nearly identical with those of southern New York. Thus, the curve flattens out when the New York level is reached, and begins to rise again only in southern Pennsylvania.

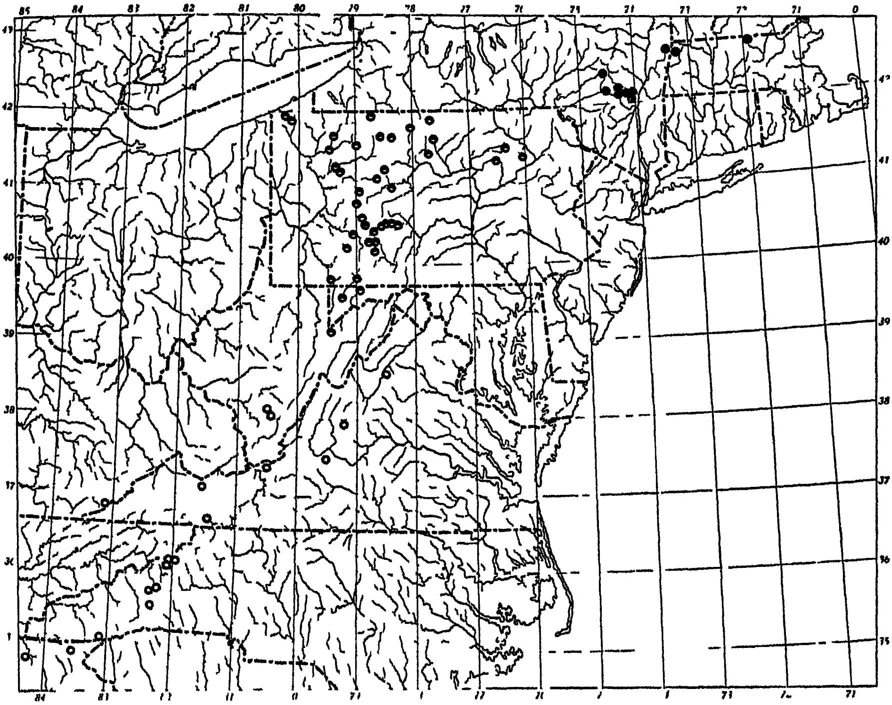

Fig. 26. Distribution of breeding juncos along the Atlantic coast. Each symbol represents a locality from which specimens have been examined. Dots, *J. h. hyemalis;* half dots, distinctly intermediate groups between *J. h. hyemalis* and *J. h. carolinensis;* circles, *J. h. carolinensis.*

Tarsus and middle toe increase fairly evenly from New England southward, with the steepness of the curve slightly greater between New York and Pennsylvania. Differences among the Pennsylvanian subgroups are not significant trends. Middle toe increases from the Maritime Provinces southward in a uniform curve of considerable steepness. Southern and northeastern subgroups in Pennsylvania are different, corresponding to the line of the general gradient.

In an earlier paper (Miller, 1938*b*), I indicated that the principal changes in averages in passing from *hyemalis* to *carolinensis* were in some instances localized more than the gradients that are here presented show. This resulted from failure in the earlier work to take into account the actual geographic spacing of the groups used. Although some irregularity exists in the gradient for bill depth, the evenness of the other gradients is striking. The present

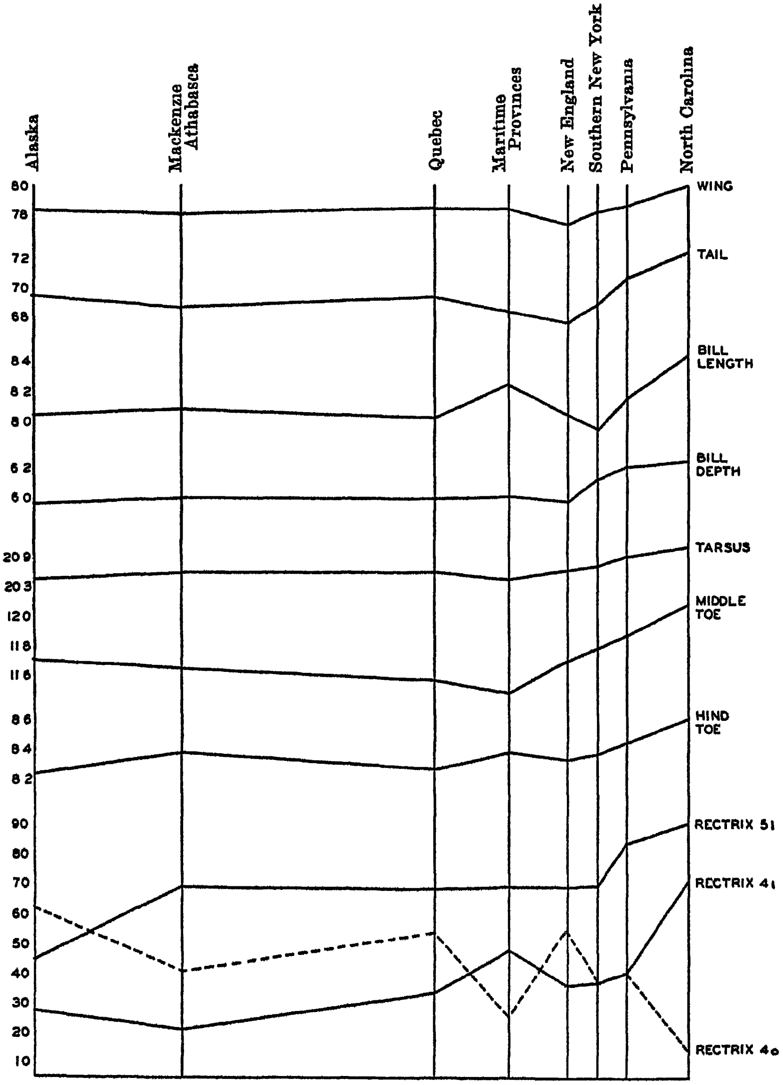

Fig. 27. Geographic variation in measurements and amount of white in tail in the transcontinental range of *J. h. hyemalis* and southward in the Appalachian Mountains to *J. h. carolinensis*. Vertical lines represent samples spaced to scale geographically. Measurements in millimeters. Figures for tail white represent percentage of occurrence of variants. 5*o*, outer web of rectrix 5 white; 4*i*, inner web rectrix 4 mixed rather than black or partly black; 4*o*, outer web of rectrix 4 entirely black rather than partly black. Males only.

analysis of the situation still shows that the gradients or changes are not perfectly coördinated. Thus wing, tail, bill depth, tarsus, and hind toe all begin to change south of New England; middle toe begins south of New Brunswick, that is, in New England; bill length begins south of New York. Gradients in measurements do not culminate north of the Carolinian area, except that of bill depth, which definitely reaches a level in southern Pennsylvania. Accordingly, the view previously presented (p. 281) that each character intergrades independently of the others is in general borne out. Some characters such as wing, tail, tarsus, hind toe, and head color may be thought of as related in their changes. But these characters are not linked or associated in individual variation, except for wing and tail, and tarsus and hind toe.

Figure 27 illustrates the increase in amount of white in rectrices 4 and 5. South of New York the remarkable uniformity in average for the inner web of the fifth is abruptly broken. There is some change between Pennsylvania and North Carolina, but much more between New York and Pennsylvania. The inconstant values for the two webs of the fourth rectrix within *hyemalis* make it apparent that the only substantial intergradational change is between Pennsylvania and North Carolina. Here, as in *shufeldti–thurberi* intergrades, the different rectrices are not coördinated in their geographic variation, even though they may be correlated to some degree in individual variation.

Summary.—Characters of *J. h. hyemalis* are remarkably uniform west to east across the continent, but southward in the mountains of the east coast there is extended gradation toward *carolinensis*. Most of the changes involved in this intergradation occur at a uniform rate geographically, despite some discontinuity of breeding populations in New York. There are three characters—bill depth, white on rectrix 5, and white on rectrix 4—that change more or less abruptly. These abrupt changes occur: one between New England and New York, one between New York and Pennsylvania, and one between Pennsylvania and North Carolina. The characters with uniform gradients begin to change: south of the Maritime Provinces (2), or south of New England (5), or south of New York (1). The only character which reaches full *carolinensis* value north of North Carolina is bill depth.

Some points of comparison with the intergradation of *J. o. shufeldti* and *J. o. thurberi* are significant. In *hyemalis* there are no gradients that run throughout *hyemalis* and on into *carolinensis*, as there are in the *shufeldti–thurberi* complex. There are more characters of *hyemalis* and *carolinensis* that grade evenly through three or four regions in the area of intermediacy. The degree of continuity of populations is about the same in the two situations. In both, not all gradients and breaks in gradients of different characters are coördinated.

How may we delimit the races *hyemalis* and *carolinensis?* As for *shufeldti* and *thurberi,* delimitation must be arbitrary if it is to be attempted. Intergradations in all characters neither begin nor end at a single point. One character does not seem more important than another. Sudden changes in steepness of gradients, infrequent in this instance, occur at different places. How can anyone name the birds from Pennsylvania? The cataloguer desires definiteness and simplicity. Unfortunately these qualities do not exist.

Because birds of New England fall so much closer to *hyemalis* than to *carolinensis,* they may be included in the former. The same may be done with those of southern New York, though they are near the halfway point between the races. Their inclusion in *hyemalis* seriously distorts the conception of that race. The Pennsylvania birds are intermediate, and little more can be said. I cannot see that they fall closer to one race than to the other by a sufficient margin, all characters considered, to warrant a rational decision.

For interrelationships with *J. hyemalis cismontanus*, *J. o. oreganus*, and *J. o. montanus*, see pages 329–343; for *J. aikeni*, page 353.

J. hyemalis hyemalis does not meet *mearnsi*. Possibly there is a near approach, or actual junction, of hybrids of *montanus* and *J. hyemalis* with *mearnsi* in the plains of southern Alberta, but as yet there is no evidence to suggest this. The area between the Cypress Hills in southeastern Alberta, where *mearnsi* breeds, and the east slopes of the Rocky Mountains directly to the west, where *montanus* occurs, probably supports no breeding juncos.

Junco hyemalis carolinensis

This race is the southern culmination of geographic variation in the mountains of the Atlantic coast. Its nature and status are to a considerable extent dealt with in analyzing its relationships with *hyemalis*. The populations from southern Virginia southward display no perceptible intensification of character and thus in this terminal area have the qualifications of a race as ideally conceived. The breeding range is restricted to the higher Appalachian Mountains, corresponding to the higher position of favorable zonal conditions to the southward. Migration, so far as is known, is limited to altitudinal movements.

Racial characters.—The color of the hood most completely differentiates *carolinensis* from *hyemalis*. A uniform light slate (type 8, see p. 247) head is nearly universal in males of *carolinensis*, whereas it is found in only 10 per cent of fully differentiated *hyemalis*. Heads of females are usually type 9, but often types 8 and 10. Thus many are difficult to segregate from *hyemalis*. Usually the gray of females is less mixed with buff or brown than in *hyemalis*. It is reported that *carolinensis* in life usually has a dark basal spot on the maxilla and that the lighter parts of the bill are light bluish horn (Ridgway, 1901, p. 282). In dried skins dark basal spots are not a constant feature, occurring in about 75 per cent. They are like those dark areas which usually border the nostril of *J. caniceps* (types 2 and 3), a feature uncommon in *J. oreganus* and *J. h. hyemalis*. For practical identification of study skins the bill color, in this instance, is of little value. Average differences in *carolinensis* and typical samples of *hyemalis* are as follows: wing, 2 per cent longer in *carolinensis;* tail and bill, 5 per cent longer; bill depth, 4 per cent greater; tarsus, 2 per cent longer; middle toe and hind toe, 4 per cent longer. There is more white in the tail of *carolinensis,* particularly among males, in rectrices 3, 4, and 5, but average differences are not great. (See p. 317 for details.)

Nongeographical variation.—But one instance of white on the wing coverts has come to my attention. Dr. Alexander Wetmore has described to me a male identified by him as *carolinensis* which was taken March 15, 1936, in the Blue Ridge Mountains of Virginia. White is present on both middle and greater coverts and even on the inner tertials [=secondaries] and, faintly, on the distal upper tail coverts. The latter feature suggests an albinistic tendency not found associated with the white-winged variants of *hyemalis*. Since *carolinensis* is in some respects a southern counterpart of *hyemalis*, as is *aikeni* of the middle west, it is noteworthy that the white-winged variation is especially rare and in occurrence parallels in no way the situation in *aikeni*.

Variation in head color is much less than in *hyemalis*, both with respect to tone of gray and to suffusion of brown and buff. The latter rarely obscures completely the gray of the sides, even in females, and is lighter colored. *Carolinensis* has a less pronounced retarded plumage with respect to buff suffusion, even though it has a characteristically pale hood, which in *hyemalis* often is a manifestation of the retarded state. The occurrence of buff with respect to age and sex presents a situation like that in *hyemalis*, and indeed other juncos, but the degree of mixture is so much less that average age and sex differences are slight.

The uniformity of the slate tone of the head is shown in the table on page 322. The exact average of tone of gray in females cannot be given, but the sexual difference is evidently somewhat less than in *hyemalis*. A situation like that in *Junco oreganus* exists, in which darker-headed races as a rule show more dimorphism in blackish pigment. Seasonal alteration of plumage is less than in *hyemalis*, owing to the lesser amounts of buff and the greater uniformity of gray both upon the individual feathers and in the different parts of the hood and mantle.

Variations in tail pattern are given on page 317.

Sexual difference in wing is 6 per cent; tail, 5 per cent; bill length and middle toe, 2 per cent. Average difference in wing and tail 10 per cent in males, 9 per cent in females.

Coefficients of variability are remarkably similar to those of *hyemalis* with respect to males. In females the correspondence is not so perfect, probably owing to the smaller sample. Coefficients of the Pennsylvania intermediates (40 birds) show no uniform tendency to higher values. The coefficients depart in varying degrees from the values typical of *carolinensis* and *hyemalis*, but apparently without regard to the degree of intermediacy of the character concerned. For certain characters the group appears to be more completely homozygous than the parental races, whereas for others it is more heterozygous, and preserves and combines the parental extremes. Among the distinctly more variable characters are wing length and bill depth, but tail, bill, tarsus, and the toes are less variable. It does not appear, therefore, that the Pennsylvania group is of immediate hybrid origin, although the apparent absence of increased variability in hybrids where many multiple factors are involved is not conclusive evidence. Diminished variability would hardly be expected, however. The genes governing dimensions in *hyemalis* and *carolinensis* must differ and it is remarkable that the same degree of variability is found in the two, especially in view of the situation in the intermediates. Is it possible that the racial extremes have reached a comparable degree of unification and adjustment to environment while the intermediates with respect to some characters have not attained this and with respect to others have surpassed it? The explanation is not obvious; the whole situation is bound up with unknown details of the history of the intermediates that are requisite to complete understanding.

Coefficients of correlation in *carolinensis* are: wing and tail, .633 ± .045; wing and bill depth, .315 ± .073; wing and tarsus, .261 ± 0.67; tail and bill depth, .378 ± .074; bill and bill depth, .364 ± .067; bill depth and tarsus, .419 ± .062; tarsus and middle toe, .258 ± .068; tarsus and hind toe, ± .171 (not significant, but compare *hyemalis*); middle toe and hind toe, .422 ± .06.

TABLE 33

MEASUREMENTS OF J. H. CAROLINENSIS

(Areas south of the latitude of the James River, Virginia)

Measurement	Sex	No. of specimens	Mean with prob. error	Standard deviation	Coeff. of var.
Wing..............	♂	79	80.25 ± .14	1.83	2.29
	♀	42	75.55 ± .21	2.06	2.72
Tail...............	♂	79	72.48 ± .17	2.30	3.18
	♀	40	68.95 ± .19	1.81	2.63
Bill length.........	♂	76	8.43 ± .03	.35	4.21
	♀	38	8.26 ± .04	.34	4.11
Bill depth..........	♂	76	6.24 ± .02	.29	4.73
	♀	31	6.21 ± .03	.28	4.53
Tarsus.............	♂	93	21.11 ± .05	.66	3.13
	♀	37	20.93 ± .07	.66	3.17
Middle toe.........	♂	86	12.08 ± .04	.51	4.20
	♀	43	11.89 ± .04	.40	3.39
Hind toe...........	♂	93	8.60 ± .03	.44	5.11
	♀	47	8.46 ± .04	.43	5.12

Some important contrasts with *hyemalis* exist. Wing and tail are comparable in the two races and the relation of parts within the foot is extremely similar. Association of bill depth and bill length, entirely lacking in *hyemalis*, suggests new common factors responsible for the large size of the bill. Some of these factors may be size-determining for many parts of the body, thus perhaps accounting for some of the correlation of bill depth with tarsus and for correlation of wing, tail, and bill depth. Wing and tail each correlate with bill length to a degree (.209 and .207) that, although not statistically reliable, seems real in light of bill depth correlations. Certain factors entering into the usual correlation of wing and tail, to the extent of a correlation value of about .2, apparently affect all dimensions of the bird. Such general factors for size are not found in *hyemalis*. It is reasonable to suppose that these factors are peculiar to *carolinensis* and that they account in part for the averages of that race.

Distribution in the breeding season.—Occurs in the Appalachian Mountain system in essentially typical form from the Potomac River to extreme northern Georgia. The lower limits of occurrence are about 3000 feet in North Carolina in the oak and chestnut forests of the mountain slopes. The limits possibly are as low as 2500 feet in Virginia, but they do not extend below 3500 feet in Georgia. Most of the population is found between 4000 feet and the summits of the mountains, somewhat over 6500 feet.

Virginia.—Blue Ridge Mountains irregularly north as far as Page County and in the Allegheny and Shenandoah mountains; generally distributed in higher mountains of the southwest.

West Virginia.—Allegheny and Shenandoah mountains from Hardy and Randolph counties south to Mercer County.

Kentucky.—Cumberland Mountains (Big Black Mountain) of the extreme southeast.

North Carolina.—Entire extent of Blue Ridge Mountain area of the far western section, above about 3000 feet elevation.

Tennessee.—Blue Ridge Mountain system along North Carolina boundary.

South Carolina.—Northwestern boundary adjacent to North Carolina.

Georgia.—Rabun, Towns, Union, Gilmer and, probably Fannin counties in the extreme north.

The forest habitat in Alleghenian and Boreal zones consists, in the lower levels, of certain of the southern hardwoods, chestnut (*Castanea dentata*), hickories, and yellow poplar (*Liriodendron tulipifera*), mixed with the northern hardwood forest associates such as beech, birch, and sugar maple, as in Pennsylvania. Evergreens of the Boreal region are chiefly red spruce (*Picea rubra*), fir (*Abies fraseri*), and hemlock (*Tsuga canadensis*). The region is one of heavy summer precipitation, the annual rainfall amounting to 50 to 70 inches. The forest floor inhabited by the juncos is arid and open compared with the habitats of *hyemalis,* with more relatively barren ground and exposed rock.

Distribution in winter.—The movements of this race in winter are extremely limited and the majority of the birds would seem to be essentially nonmigratory. It is reported that they move down the mountains to winter in the lowlands. There are, however, midwinter records in abundance from such mountain localities as Black Mountain and Craggy Mountain, North Carolina. The danger of confusion with misidentified wintering *hyemalis* is great. Among winter birds, personally studied, I have seen none that was certainly *carolinensis* that was taken in the piedmont region more than a few miles from the bases of the mountains. Numbers of lowland specimens considered to be *carolinensis* prove to be *hyemalis* or of doubtful origin with respect to breeding area.

Junco hyemalis cismontanus and the relationships of Junco hyemalis and Junco oreganus

The relationships of *Junco hyemalis* and *Junco oreganus* need to be fully elucidated to explain the complicated plumages that apparently result from interbreeding of these species. The status of the race formerly called *J. hyemalis connectens* by Swarth (1922, p. 244), which now must go by the name *cismontanus* Dwight (see Appendix, p. 403), is a part of this problem. To anticipate conclusions, it may be stated that *cismontanus* is a fairly uniform group of birds, doubtless of hybrid origin to begin with, which now perpetuates itself independently of further hybridization of the parental types, *J. oreganus* and *J. hyemalis. Cismontanus* on the margins of its breeding range breeds freely with *J. h. hyemalis,* which it most resembles. In certain regions it does not interbreed freely with *J. oreganus,* whereas at other localities hybridization is evidently frequent. As pointed out elsewhere in connection with possible origin of forms through hybridization, the degree of uniformity, geographic segregation, and the autonomy from the related or parental forms are the criteria for judging of the existence of a race; the mode of origin is not significant. The probable genetic identity of members of a race such as *cismontanus* with newly produced hybrids of the parental types is not denied. The logical mode of analysis of *cismontanus* is first to deal with all *oreganus–hyemalis* hybrids and then proceed to the formal, practical circumscription of the race, even though this procedure may not pattern after the treatment accorded other races.

Characters which are practicable for analysis in *oreganus–hyemalis* hybrids are those of color. Dimensions and the white areas of the tail are similar in *J. h. hyemalis* and *J. oreganus montanus* so that in treating of small groups of individuals little can be said concerning them. When *J. hyemalis* and *J. o. oreganus* interbreed, dimensions are worth considering. The color areas concerned are the head, sides, and back. Each of these shows interesting complications in hybridization. Lines of demarcation, as at the junction of the hood with the sides and with the back, are to some degree the result of combinations of conditions in the separate areas. The relation of hood and sides is comparable to that found in *J. c. caniceps–J. o. thurberi* hybrids.

The most striking difference in color is in the sides, which in *J. hyemalis* are slate and in *J. oreganus* are wood brown or pinkish brown. Although the latter species does not have distinct gray areas in the side feathers (for rare exceptions in *J. o. oreganus* see p. 271), a considerable amount of eumelanin may be mixed with phaeomelanin to produce dark brown. In *hyemalis,* in the retarded plumage, the slate of the sides may be partly or completely replaced by brown so that they are indistinguishable from the sides of *oreganus,* although the distribution of pigment granules in the barbules is somewhat different (see p. 313). If the plumage of *hyemalis* is thus retarded, the hood is equally affected and the color areas are confluent. In retarded plumages of *J. oreganus* the demarcation is visible beneath the buff feather tips. The part of the side immediately adjoining the hood constitutes the critical area where differentiation between the species in all plumages may be sought. The close approach of many female *hyemalis* to *oreganus* makes it much more difficult to allocate females than males, even though genotypically there probably is as much difference in the females as in the males of the two species.

In males, obvious hybrids show nearly every degree of mixture of slate and brown. The two colors are segregated into different areas of the feather vanes. The anterior part of the side area is more prone to slate color, the posterior region to buff and brown. No occurrence has been found of an anterior section browner or buffier than the posterior section.

Such differentiation within the side area was not found in *caniceps–oreganus* hybrids. The *hyemalis* condition seems to involve a gradient of slate color from the head to the sides; in *oreganus* this gradient is broken and the sides are autonomous. To modify these regions in the direction of *oreganus* (1) the gradient must be interrupted and (2) phaeomelanin must replace (or nearly replace) the slate-producing eumelanin. In hybrids of *hyemalis* and *oreganus*, then, the degree of contrast of head and sides may not be solely the summation effect of different colors in the two areas. The independence of the gradient and pigmentation factors is shown by hybrids in which the sides are pure gray yet distinctly marked off from the dark slate of the hood, and by others with buff or brown sides which anteriorly have some slate that grades into the hood. There are also birds with mixed gray sides that do not grade evenly into the hood.

An additional interrelation of hood and sides is shown in hybrids in which the sides are to a varying extent gray and the typical *hyemalis* gradient is manifest, but in which the *oreganus*-like darkening of the eumelanin of the hood is also reflected in the sides. A comparable intensification effect was seen in the eumelanin of *caniceps–oreganus* hybrids uncomplicated by the gradient effect of *hyemalis*. To summarize, three sets of controls are operative in the hood-side complex: determination of slate or buff-brown in the sides; presence or absence of a tendency to a gradient of color between head and sides; and a common intensification of the eumelanin of head and sides. A particular situation with respect to one set of factors may modify or mask the expression of another set.

In the *hyemalis–oreganus* hybrids there is nowhere a fully isolated hybrid population that appears to have been set up in the simple fashion of the *caniceps–thurberi* hybrids of southern Nevada. One cannot assume, as in the *caniceps–mearnsi* hybridization in Utah, a bilateral infiltration of parental types into the zone of hybridization, because the obvious hybrids are more irregular in distribution and there is some restraint of hybridization. Consequently, it is not safe to draw positive conclusions from evidence of phenotypic combinations concerning the dominance of characters or the degree of simplicity of the factorial mechanism. In at least two regions where populations occur that are predominately of *hyemalis* character, but with some evidence of mixture, the proportion of *oreganus* characters in the sides to *oreganus* characters in the back is 7 : 13 and 4 : 8. These populations are from the Cassiar (Stikine to Carcross) and Jasper Park sections, respectively. They do not mix freely with *oreganus*, and perhaps they were established from a particular hybrid group which through segregation had more *oreganus* back characters than side characters. But it is remarkable that two samples from well-separated areas should show such similar ratios. It would appear possible that in males there is some degree of dominance of *hyemalis* sides over *oreganus* sides. In the scattered hybrids closest geographically and phenotypically to *oreganus* there is an apparent preponderance of *hyemalis* sides relative to *hyemalis* back, so that the suggestion of dominance is borne out.

The sides of females present a different situation. Buff- or brown-sided hybrids may owe their resemblance to *oreganus* to a retarded *hyemalis* state or to *oreganus* factors. The tendency already present in *hyemalis* to show buff sides seems to lead to *oreganus* coloration if any *oreganus* factors are present.

Thus slate sides are not dominant or at least do not appear with great frequency, because of interaction of sex factors or hormones in females. As Swarth (1922, p. 244) has pointed out, the females from the Cassiar area resemble *oreganus* much more than do the males. Out of 41 males of the Cassiar area, 7 showed some buff in the sides, but out of 32 females from the same region 26 showed some buff. The confluency of head and sides is another matter, however. Occurrence of an even gradient in side and hood color is essentially as frequent in females as in males in groups of dual affinity. Still, the prevalence of buff sides in the females gives a mass effect much more like that of *oreganus* and tends to obscure, and draw attention away from, the gradation of the color areas.

The heads of males of both species vary considerably and the range of intensity of eumelanin overlaps in northern *montanus* and *hyemalis,* both forms possessing variants classed as type 6 (dull black or dark slate). The extent of the dark areas, if identical in tone, is never the same. The darker *hyemalis* variants do not, with rare exceptions, show extension of the black over the nape to a definite transverse line in front of the interscapular area. In hybrids there are, therefore, extensions and intensifications of varying degrees, increasingly toward *oreganus.* The intensification shows a finely graded series of intermediate stages, as in other similar situations within the genus, and presumably there is a series of multiple factors operative. The extension posteriorly is independent of intensity, although of course if the pileum is light slate there is no contrast with the rest of the head and no extension can be seen. Intermediate stages in extension are numerous, but they do not appear as progressive changes in position of a sharp line of black, but as progressive suffusion of darker color back over the neck to a definite line which, with greater intensity of black, becomes more and more apparent. In females comparable changes take place, complicated by buff tipping and lighter tones of gray, slate, and black. The buff tipping is more uniform in *hyemalis* and is complementary in part to the dark slate of the forehead, so that in a sense a uniform brown neck and pileum is equivalent to a uniform slate dorsum. Retreat posteriorly of the heavy brown tipping is the counterpart of posterior extension of the dark slate or black in male, or advanced female, plumages.

Pigments of the back consist solely of eumelanin in advanced male plumages of *hyemalis,* except for the extreme feather tips, which rapidly wear away. Just proximal to these tips is a zone of pale gray, and farther proximally is the true slate area that is the dominant color in worn plumage. In hybrids with *oreganus,* phaeomelanin, not unlike that of the extreme tips, extends into the outer gray zone, modifying the light gray to produce light brown. This gives a spotted appearance to the back when the basal slate parts are exposed through wear. A further influence of *oreganus* is manifested in progressive reduction of the basal slate or blackish areas until a fairly uniform brown feather results (type 3*b* of *montanus*). Some reduction of the basal slate areas may occur without the addition of phaeomelanin, but the area is never fully replaced merely by light gray. Some brown feathers appear to have an unusually large amount of eumelanin mixed with the phaeomelanin (type *3a*) throughout the vane, but usually any increment of eumelanin in *oreganus*-like feathers appears basally without toning down the brown beyond *3b*. Most of the *montanus* that are classed as *3a* have small basal slate spots attributable to *hyemalis*. Increased black or slate basal spots are classified as *a, aa,* and *aaa.* The last two types are found in typical *J. h. hyemalis*. Sometimes phaeomelanin of intensity 1 or 2, as well as 3, is combined with *aa,* and rarely with *aaa.*

It has been noted that hybrids with *aa* or *aaa* pattern and with black *oreganus*-like heads may "reflect" the dark head color in these basal feather spots. The general intensification of eumelanin is thus comparable to that which is seen in the slate of the sides. Invasion of the back by phaeomelanin always takes place over the whole area, and as this pigment increases the back becomes sharply contrasted with the head.

The line of demarcation of head and back is then the result of phaeomelanin of the back and the intensification and extension to a definite neck line of the black of the dorsal part of the head. A line may be distinct as a result of contrast of black neck and gray back (slate, with light gray margins), or by contrast of slate neck with brown backs *3b*, *3aa*, or *3aaa*. There is no gradient factor, as there is between hood and sides. The most striking contrast naturally results from combined black neck and *3b*, or, even better, *oob* (*J. o. oreganus*) or *1b*.

In fresh overcast plumage, much of the contrast of back and head may be obscured, but it never disappears in pure-blooded *J. oreganus*. In female *hyemalis* the extension of buff far basally on the back feathers often results through wear in a brown back patch in the breeding season. Such a patch usually is not sharply defined; yet it is much like a *3b* or *3a montanus* back. In the Cassiar group, brown-backed females of this sort plus those of *oreganus* blood make up a large group of females that resemble *oreganus,* both with respect to the back itself and the contrast of the head. Thirteen of 41 males have no type 3 phaeomelanin, whereas 25 out of 32 females possess it. This difference is not truly a matter of dominance of *hyemalis* character in males that is lacking in females, but results merely from the phenotypic identity of retarded plumages of *hyemalis* and hybrid back types. With respect to sides, the even greater sexual difference (♂, 7 with *oreganus* character out of 41, and ♀, 26 out of 32) is probably a summation effect of differences in dominance in the two sexes and similarity of *oreganus* and its hybrids to the retarded female *hyemalis* plumage.

The colors of head, back, and sides appear to assort independently in hybrids except that when eumelanin is present in two or more areas intensification may be correlated. Probably few hybrids of the F_2 generation from pure parental types exist, so that the full amount of assortment is not often seen. Most interbreeding is probably between types one or both of which already is heterozygous. This situation, together with multiple factors and intensification factors, obscures the typical aspects of assortment.

With respect to distribution, intermediate birds fall chiefly into two classifications, namely, (1) those populations either out of contact, or not freely mingling, with *J. oreganus* which nevertheless are of hybrid ancestry, and (2) scattered individuals of more immediate hybrid origin either in the zone of contact between *J. oreganus* subsp. and the birds of class 1, or at localities distant from such regions. Group 1 differs in uniformity in different regions, but its characters partake more of *hyemalis* than of *oreganus*. In general it occupies the eastern foothills of the Rocky Mountains and the edge of the plains from the vicinity of Jasper Park northwestward, extending into the Stikine and Taku drainages east of the coast range to the Atlin area. Along its western margins it meets *J. oreganus* geographically, but there is evidence to show that it does not freely interbreed. There is nothing comparable in

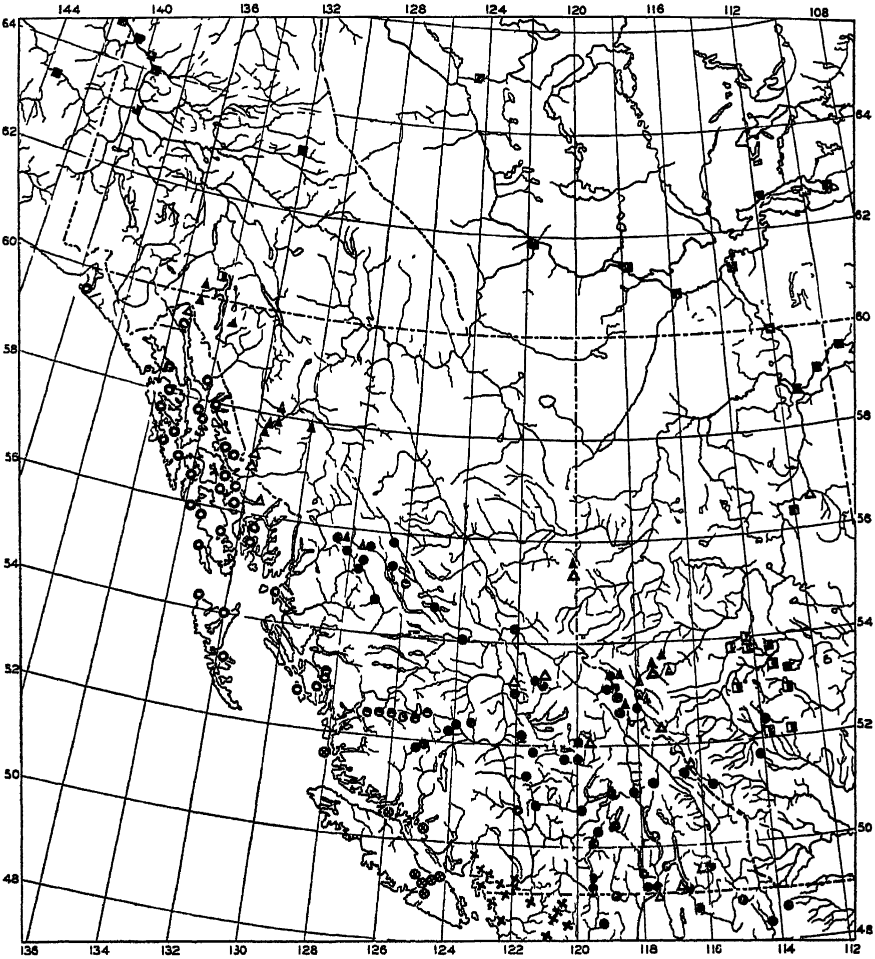

Fig. 28. Distribution of breeding juncos in western Canada and southern Alaska. Each symbol represents a locality from which specimens have been examined. Dots, *J. o. montanus;* half dots, intermediates between *J. o. montanus* and *J. o. oreganus;* plain circles, *J. o. oreganus;* circles enclosing crosses, intermediates between *J. o. oreganus* and *J. o. shufeldti;* crosses, *J. o. shufeldti;* open triangles, hybrids between *J. oreganus* subsp. and *J. hyemalis* subsp.; solid triangles, *J. h. cismontanus;* half-open squares, intermediates between *J. h. cismontanus* and *J. h. hyemalis;* solid squares, *J. h. hyemalis.*

the way of a group that is chiefly of *oreganus* type but with all individuals to some extent intermediate. The sharpest division between *hyemalis* and *oreganus*, then, is one between *J. o. oreganus* or *J. o. montanus* and *hyemalis*-like birds already to some degree possessed of *oreganus* blood.

In southern interior Alaska occasional evidence of mixture (usually reported as *montanus*) is found in populations otherwise of pure *hyemalis* type; the same is true of the Slave River Valley and probably of parts of Yukon Territory. Localities of such occurrences which I have verified are: mountains near Eagle, Alaska; Fort McMurray, northern Alberta. The bird from the latter locality (no. 231616 Mus. Comp. Zoöl.) was taken May 8, 1920; the ovaries were "scarcely enlarged," so that this may be another instance (see p. 240) of a stray migrant. It again suggests how intermingling might take place at localities remote from the regions of hybridization or intergradation. Dwight (1918, p. 295) mentions "*montanus*" occurring far north in the Mackenzie Valley. No details are given, and I have not been able to verify such an occurrence although essentially all the material that Dwight studied has passed through my hands.

In south-central Yukon Territory, south of Lake Marsh, *oreganus* characters in the *hyemalis* population become frequent. From Carcross, Yukon, and Bennett City and Atlin, British Columbia, a considerable series is available. Out of 54 summer resident birds only 8 are without some *oreganus* character; none is typical of *J. o. oreganus*, which breeds in the coastal belt just west of the coast range. Among males of this area, the sides of 31 are pure slate or blackish slate; the remaining 4 are mixed with brown, but slate predominates. The ventral hood color ranges from type 4 to 8 intensity, with an average of 6.4 compared to 4.0 in northern *montanus* and about 7 in *J. h. hyemalis*. The intensity of black on the pileum is slightly greater than in *hyemalis*, the modes of occurrence being dark slate and slate, instead of slate; light slate (2) and black (4), deeper than the dull black of *J. h. hyemalis*, occur. The black, irrespective of intensity, extends to a neck line to contrast distinctly with the backs in all but 7 of the males; 4 of these are fall birds in which overcasting obscures what might otherwise be a fairly sharp contrast. With respect to the back, only 1 shows type *a* eumelanin; the rest are *aa* or *aaa*. Type *aa* is not common in *J. h. hyemalis*, but it is frequently found in these populations. Type 3 phaeomelanin occurs in 8 out of 31 males. In summary, all characters of males of this region are distinctly closer to *hyemalis* than to *oreganus*. In each color area, not more than one-fourth are really different from *J. h. hyemalis*. But with respect to extension of black of neck posteriorly to a definite line, 80 per cent are distinct from *hyemalis*. This is probably the situation because any one of three *oreganus* characters (extension of black on nape, brown back, or especially dark head) will set up some degree of *oreganus*-like contrast.

The only evidence for interbreeding of this adulterated *hyemalis* stock of the Atlin sector with *J. o. oreganus* is supplied by a specimen (no. 165749 U. S. N. M.), from Glacier, White Pass, Alaska, north-northeast of Skagway in the pass leading to Lake Bennett in the interior. The locality is in the center of the coast range. This bird has sides that are mixed with gray only anteriorly, the head is type 7, the pileum is dull slate and extended to a neck line, and the *ooa* back is sharply contrasted. Type *oo* phaeomelanin never seems to appear except close to the range of *oreganus,* and of course it would never be derived from intermixture with *J. o. montanus.* This hybrid has a wing 76.0 mm. long, which is below average for *hyemalis* and above average for *J. o. oreganus.* The foot is not conspicuously large as in *oreganus,* but the tail pattern is that of average *oreganus.* The abundance of such obvious hybrids in this region is unknown. Probably the population is sparse but largely hybrid, in view of our knowledge of similar situations that obtain in the lower Stikine River to the southward. It is suspected, but not known, that hybrids like this also occur in the somewhat limited suitable territory between the interior and coast in the Alsek and Taku river valleys to the north and south. In the north there might be a direct meeting of *J. o. oreganus* and typical *J. h. hyemalis.*

One hundred and fifty miles south of Atlin in the interior Stikine River basin another group of breeding juncos has been taken. Swarth (1922) based his concept of the Cassiar junco on this group and gave a rather complete description of the nature of the population. However, it is necessary to review the group in terms of the analysis of variants employed in this work. Juncos were taken at Telegraph Creek, Glenora, and Dock-da-on (*op. cit.,* p. 129), all places well within the interior biotic province. There were 18 males and 15 females.

This group closely resembles the Atlin series, but upon careful analysis it proves somewhat more homogeneous. It includes only one individual, a female, that might be confused with *J. h. hyemalis.* Yet among the males there is no individual that could be confused with *J. oreganus* subsp.; there are only two such females and they probably possess *hyemalis* blood. Certainly this group is not one that has arisen from immediate hybridization of parental types, or else these parental types would be present in some quantity in the population.

Of the 18 males, 4 have some brown in the sides. The hood varies from 5 to 7, average 6.1. The intensity of black of the pileum varies from dull black to slate, much as in the Atlin group, but 10 individuals are dull black, so that there is less average variation and a single mode of higher value. Black or dark slate extends to the neck line to contrast with the back in all but 1. There is only 1 type *b* back, no type *a,* and about half and half *aa* and *aaa.* There are 9 with type 3 phaeomelanin, a higher proportion than at Atlin (8 out of 31). The principal differences in the Stikine group are, then, more uniform head color, above and below, more constant neck line, and absence of *hyemalis*-like types, which latter factor increases slightly the percentage occurrence of *oreganus*-like back and side characters. The heterogeneity, though easily perceived, and more prominent than Swarth indicated, is no greater than in *J. h. hyemalis, montanus, shufeldti,* or *thurberi.* This similarity to situations in other forms of juncos led Swarth appropriately to conceive of the group as a race, even though he could not determine its geographic limits.

Westward, down the Stikine River, Swarth endeavored to obtain breeding birds at Flood Glacier and Great Glacier, where, however, they were scarce. The former locality is in the area of transition toward coastal conditions. Eight adults from this place show distinct mixture of characters. The combination of characters in these and in two birds from Great Glacier (nos. 40002, 40004), which is farther down stream where there are coastal conditions, is as follows.

M.V.Z. no.	Sex	Sides	Lower surface of head	Upper surface of head	Back	Wing	Bill depth	Middle toe
39988	♂	slightly slate	6	dull black	*2b*	77.0	6.3	11.2
39990	♂	buff-brown	6	black	*1b*	79.8	5.7	11.1
39998	♂	slate	5	black	*1a*	77.0	6.4	10.8
39993	♂	slate	6	dull black	*2a*	77.5	6.6	11.5
39987	♂	buff-brown	5	black	*1a*		5.7	11.1
39999	♂	slate	6	slate	*aa*	77.8	6.1	11.6
39994	♀	buff-brown	6	slate	*oob*	69.0	6.2	11.3
39991	♀	buff-brown	7	slate	*oob*	73.0	5.8	11.4
40002	♂	buff-brown	5	black	*1b*	78.3		11.7
40004	♀	buff-brown	6	slate	*oob*	71.6	5.9	11.5

Some of the Flood Glacier birds are truly hybrids. Both parental types are present, and also birds with various mixtures and assortments of characters. Side color in males seems to segregate more than back color, which tends to be intermediate (*1b*, *1a*, *2b*, *2a*) between the extremes (*aa* and *oob*). Dominance of slate sides in males is suggested even by this small sample. Only 1 typical *aa* back occurs to 3 slate sides. Most of the wing lengths are variously intermediate (multiple factors); bill depth and middle toe show a rather great variation for so small a sample.

Swarth was much concerned with the resemblance of the backs of these hybrids to *montanus* (= *shufeldti* of Swarth). He felt it to be impossible for *montanus* to extend northward between his *connectens* (= *cismontanus*) and *J. o. oreganus* on the coast, and for that reason discounted the possibility that *montanus* contributed to these birds. I believe Swarth overlooked the tendency for juncos to inhabit timber-line and subarctic terrain. McCabe and others have found juncos nesting above timber line in the coastal mountains. A more cogent reason for believing that these *montanus*-like birds are *J. o. oreganus* × *J. h. cismontanus* is the fact that both parental types are present at Flood Glacier. The *montanus* type of phaeomelanin, No. 3, already is common in *cismontanus*. If now additional *oreganus* factors, irrespective of race, are added that reduce the eumelanin, *3b* or *montanus* type of back results. Types 1 and 2 of phaeomelanin that occur in *montanus*, but not in *cismontanus*, are certainly to be considered as intermediates from the breeding of type 3 with *oo* of *oreganus*. One of two birds from Great Glacier has a *1b* back, again probably because of hybrid ancestry. A *montanus*-like bird, with type 1*b* back, from Bradfield Canal, Alaska, probably is of similar origin.

Two hundred miles south of the Stikine River in the upper Skeena Valley, *montanus* is the summer resident junco, so that somewhere in the interval *montanus* must push north between *J. o. oreganus* and *J. h. cismontanus.*

Of 54 *montanus* taken in the Skeena region (some fall birds, but probably all near their breeding grounds) only 1 has *hyemalis* character and this consists only of a small amount of gray anteriorly on the sides. However, two pairs of *cismontanus* were seen by Swarth, and a male and female, not necessarily a pair, were taken. Both these are completely slate sided; 5 and 7 (♀) with respect to head below, and above, dull black and light slate (♀); the backs are 3*b* and *aa* (♀). Swarth in his notebook speaks of the *"connectens"* being in pairs and implies that members of the pairs were equally well-characterized slate-colored juncos. The implication that the two types do not interbreed is borne out by the rarity of birds of decidedly mixed characters such as the one mentioned which had a small amount of gray in the sides. Surely more of this type should appear if the *cismontanus* that were there interbred freely with *montanus.* Interbreeding should result in a complex something like that in the Flood Glacier district of the Stikine Valley.

The next region to the south that is well represented by birds comparable to those of the Stikine is the Jasper Park area of the Rocky Mountains. Here a different geographic situation prevails. *Cismontanus* occupies the east slope of the mountains primarily, while *montanus* is on the west slope. There is no isolated intermontane basin for this group of *cismontanus*-like birds to occupy.

From a transection from Edmonton through the continental divide at Jasper Park to the headwaters of the Fraser River there are 43 breeding males and 17 females available. Those in the plains area, from Edmonton south and west about 80 miles, constitute a unit (11 males, 5 females). In this group only 1 male has a mixture of brown in the sides. The hood varies from 6 to 8 and averages 6.3. The color of the pileum varies from dull black to slate, with the mode at dull black (5). Black or dark slate extends from the back to the neck line to contrast with the back in 6 only. There is but 1 type *b* back and no *a;* the others are chiefly *aaa;* there are only 2 with type 3 phaeomelanin.

This group has a lower percentage of *oreganus* characters than does the Atlin series. The females likewise bear this out. Only in the intensity of head color do the males equal or (dorsally) surpass the average of the Atlin series. The more fundamental characters of sides and back are more uniformly like *J. h. hyemalis.* It should be recalled that north and east of Edmonton birds appear to be typical of *hyemalis,* except for sporadic *montanus*-like birds, as at Fort McMurray (see p. 335).

Along the base of the Rocky Mountains, and extending up nearly to the divide, is a piedmont region from which there are 19 males and 4 females. This zone is about 130 miles wide, but most of the specimens are from the westerly half of this sector. As Riley (1912, p. 68) has pointed out in reporting on the juncos of this area in the collection of the United States National Museum, most of the birds of these eastern slopes are like *hyemalis,* that is, in present terminology, *cismontanus*. In comparison with the Edmonton group, 6 out of the 19 males have some brown in the sides. Two of these have no gray in the sides and no other *hyemalis* characters whatsoever. Two others have more brown than gray in the sides, but obviously are of mixed parentage. The 2 birds that are seemingly *montanus* in all respects may be left out of the comparison, for it is possible that they were more or less isolated sexually from the *cismontanus*-like group. In the remaining 17 the hood averages 6.3, as in the Edmonton district, although type 5 variants appear. Dorsally the situation is comparable, the mode is dull black, as at Edmonton, but black variants are added. Only 3 show indistinct contrast of head and neck. Back type *b* is absent, but 3 are of type *a* and the rest are divided about equally between *aa* and *aaa*. Type 3 phaeomelanin occurs in 6.

This group shows no average increase in head pigmentation compared with the Edmonton group, but a few darker variants appear. However, *montanus*-like backs and sides are much more common, reaching a frequency of occurrence roughly equivalent to the Atlin series. The uniformity of character lies somewhere between that of the Atlin and Stikine series. *Montanus* characters are no more prevalent than at Atlin, but pure *hyemalis* are less frequent. There are only 3 males that could be confused with *J. h. hyemalis*. Among the females, 2 are in all respects *montanus*. The other 2 are of mixed character.

The third group (13 males, 8 females) in this transection come from Yellowhead and Moose passes along the continental divide, or from points in the mountains not more than 10 miles west of the divide. All the females and 10 of the males are indistinguishable from *J. o. montanus*. The other 3 males are possessed of full slate sides, 6 or 7 type of head, dull black to slate pileum, *aa*, 3*aa* and 3*a* backs. All three come from the passes, not west of them. They are as strongly *cismontanus* as are any birds from the eastern slopes of the mountains.

This abrupt appearance of *J. o. montanus* in essentially unmixed populations as soon as the high mountains are entered is remarkable. Nowhere else in the genus do two such distinct forms come into such contact and fail to interbreed freely (compare *J. c. caniceps* and *J. o. mearnsi*, or *J. c. caniceps* and *J. o. thurberi*). The localities in the passes where the three males of *cismontanus* were taken and the two localities (Henry House and 15 miles south of Henry House) where *montanus* occurred east of the divide do not produce birds of the decidedly mixed type such as are found in the lower Stikine River, where *cismontanus* and *J. o. oreganus* hybridize. However, there must be some hybridization, else it is difficult to explain the increase in *montanus* characters westward in the foothills from Edmonton. The situation may be similar to that in the Skeena region (Kispiox Valley) where Oregon juncos segregate with their own kind, yet occasionally cross with *cismontanus*. In the Jasper region the sharp ecological differentiation of the plains and mountains, in addition to the probable sexual intolerance of the species, may aid in keeping the two types separate.

Some speculation concerning the nature of the intolerance may be in order, even though little critical evidence can be brought to bear. The similarity of females of the two species suggests that if plumage is important, it would be easier for females to distinguish males than for males to distinguish females. In captivity, males of different species seem to be responsive to any kind of female junco, but several females have shown no interest in males of different species; there may, however, have been other factors than preference and recognition of species that inhibited the females. Nevertheless, selection or recognition by females is possibly the controlling factor. A female *montanus* thrown in the company of *J. h. hyemalis* exclusively might be receptive, as indeed they sometimes appear to be in captivity, but if some *montanus* males were present they might be preferred. The same might hold for females of *hyemalis,* although it is possible that the females of one species are more discriminating than those of the other.

One hundred and sixty miles northwest of Jasper Park in the Peace River district in the Tupper Creek region, latitude 55° 30′, longitude 120°, a small sample taken by Cowan (1939, p. 59) is about equivalent to the birds of the piedmont area of the Jasper Park transection. One of 4 males is close to *montanus* and one of 4 females is identical with that race in back, side, and hood pattern. The other 6 correspond well with the Atlin series. Backs are *a* to *aaa,* and sides slate or predominately slate. It is not certainly known whether the *montanus*-like birds in this sector remained somewhat segregated from the slate-colored birds. Indications on the labels with respect to mated pairs suggest that they may.

One hundred miles west of Jasper Park in the Barkerville region *montanus* is the summer resident form. Yet here, within a series of 26 breeding male birds, there are 4 with some *hyemalis* character. These are: no. 448 McCabe collection, with slate sides, head 5, pileum black, neck line distinct and 3*a* back; no. 65708 Mus. Vert. Zoöl., with brown sides, head 3, pileum black, neck line distinct, and 2*aa* back; no. 186 McCabe, with slate sides, head 2, pileum black, back 3*aaa;* no. 65711 Mus. Vert. Zoöl., with sides mixed, but predominantly brown, head 6, pileum black, neck line distinct, and 3*b* back. Two of these birds, which I took, did not possess enough *hyemalis* character to be recognized as such in the field. Evidently these two arose from hybridization. Individuals of *cismontanus,* common in migration in this area, if they lagged behind to breed, would not find their own kind among the great numbers of *montanus* and consequently would hybridize, whereas such birds would not usually be "forced" to do this in the Jasper region, nor perhaps in the Skeena Valley.

Although mountains are rarely barriers to juncos, they may influence dispersal in the breeding season in the north. Spring migratory movements seem to be along the lowlands, and thence upward as the snow retreats to timber line. Thus, in the Jasper area *cismontanus* moves up the eastern slopes in spring and abruptly meets *montanus* that has come up through the lower parts of the western mountains. Along the Fraser Valley and in the Skeena area there is a northward migratory flow of both types, each going to its own breeding grounds. This movement along the same line may facilitate mixture.

South of the Jasper Park area, along the eastern slopes of the Rocky Mountains, the slate-colored types do not dominate. This might be expected because *J. h. hyemalis* is not found eastward of this region. Few specimens are extant, and it is probable that juncos are not widely distributed or abundant in the foothills about Calgary. One female from Didsbury is indistinguishable from *montanus,* but in this sex this means little. From Banff, just east of the divide, 10 males and 2 females have been examined. Only one male has mixed sides; 1 has slate sides; the others have *montanus* sides. Heads of males average 5.3 (4 to 7), somewhat paler than in northern *montanus* (4), but distinctly darker than in *cismontanus* of Jasper (6.3). All heads and backs are well contrasted. All backs but one are type *b* and phaeomelanin is for the most part type 3, with variants 1 and 2 present. Thus the group is chiefly *montanus,* nearly as much so as is the Barkerville group, and it is equivalent to the group found in and west of Yellowhead Pass.

West and south of Banff in the East and West Kootenay districts, scanty evidence indicates that the populations are similar to the one at Banff. They are essentially *montanus,* with occasional hybrids. Since there are no populations of *hyemalis* in the vicinity, these hybrids must be the result of interbreeding of stray *hyemalis* or *cismontanus* with *montanus.* As at Barkerville, far from populations of pure *hyemalis* or *cismontanus,* nothing seems to deter free intermixture. Male birds, entirely of *montanus* character, have been examined from Revelstoke, Summit, Glacier, and Field. A bird with partly gray sides and 3*aaa* back from Cranbrook, and one each with some gray in the sides (one with 3*aa* back) from Clearwater River and Rossland, B. C., have been seen. At the last two localities named, other birds are all *montanus.* Two birds from Creston near the Idaho line have partly gray sides, and a third has a 1*aa* back; 14 breeding birds from this area have been examined. South of the Canadian border in Montana and Idaho no conclusive evidence of mixture has come to my attention. One bird from the Clearwater River, Idaho (no. 61682 Mus. Vert. Zoöl.), has type *a* back, but the back is not spotted with distinctly outlined dark areas. It may be a variant unrelated to *hyemalis.*

Summary.—Hyemalis and *J. oreganus* hybridize when individuals of one type, for various reasons, occur among populations of the other. This results in the widely scattered occurrence of hybrids, for each species may wander far into the range of the other. When the two species both occur in numbers in a region, they tend to segregate and mate like with like, although even here some hybridization may take place. Through occasional hybridization (involving probably the race *montanus*), modified *hyemalis*-like populations (*J. h. cismontanus*) have been established adjacent to *J. oreganus* subsp. Certain *montanus* characters are spread fairly uniformly through it. The modified groups behave toward *J. oreganus montanus* as indicated above, that is, they do not interbreed freely at points of junction. The groups differ in uniformity. The group in the inner Stikine Valley is especially stable where it is partly isolated from *J. oreganus* and from pure populations of *J. h. hyemalis.* Quite probably these *cismontanus* groups have arisen at different times. In some, new intermixture of pure *oreganus* and *hyemalis* may still be taking place; others may have been established much earlier. With the retreat of the glaciers and the opening up of an intermontane area in the north, some modified *hyemalis* individuals that arose from interbreeding farther south may have moved in to take possession to the exclusion of the parental types. Being isolated, the characters of the original stock remained undiluted and their average occurrence about the same. The heterozygosity of the original stock would, through segregation, occasionally give rise to birds that resembled the parent types in a number of characters.

This probable course of events in the history of the Stikine and Atlin groups is what was predicated as necessary for the establishment of a race in the *caniceps–thurberi* zone of intermixture. In this zone the conditions were not quite right for isolation of a yellow-backed hybrid. In *cismontanus* a further step was made, and a race unit of appreciable extent and fair uniformity has resulted. In *dorsalis,* a race thought to be of hybrid origin, the uniformity and isolation are more nearly perfect. No longer does hybridization occur; the initial formative stage is passed, and the race may continue to evolve independently.

The striking thing about *cismontanus* is that in different areas one can see the genetic type produced in nature by hybridization and at the same time in other places see the same type (phenotypically at least) isolated to a fair degree and expanded into fairly uniform populations which compare favorably in all essential qualities with other races of juncos. Rare indeed are such opportunities of seeing the origin of a race and the "finished" product at the same time.

It is worth noting again that an *oreganus*-like group with some *hyemalis* characters mixed uniformly through it has not appeared. Several reasons may be suggested for this. *Hyemalis* may not have moved into the territory of *oreganus* so much as *oreganus* has moved into *hyemalis* territory. Or, hybrids may compete more successfully with *hyemalis* than with *oreganus.* On the other hand, *cismontanus* may be more exactly intermediate genetically than would appear. In the male the sides of *hyemalis* type show evidence of dominance. The partial intolerance of the species might rest on this feature, so that despite its hybrid nature *cismontanus* would on the average breed with *hyemalis* more than with *oreganus.* This would lead to accumulation of more *hyemalis* characters and make *cismontanus* tend even more toward *hyemalis.* The greater importance of specific recognition marks in the males is a premise in this line of reasoning. If this latter explanation is correct, it is not surprising that populations of *oreganus*-like intermediates (*transmontanus* of Dwight) do not exist.

As a practical matter it seems wise to continue Swarth's practice of according the Cassiar populations (*"connectens"*) definite nomenclatural status as a race. It seems that this group, though clearly of hybrid origin, has passed the formative stages and now in certain districts is a race. The naming of the large group of birds of this type would be difficult unless this procedure were followed. The reasons for the use of the name *cismontanus* in place of *connectens* are given in the appendix on nomenclature. Since genetically, and certainly phenotypically, birds of immediate hybrid origin are identical with those of relatively uniform breeding populations of *cismontanus,* all birds of this appearance must be designated by this name when on the wintering grounds or in migration. Generally I do not favor the practice of considering a bird apart from the breeding population of which it is a member. For example, it does not seem reasonable in the chickadees for intergrades of *P. atricapillus septentrionalis* and *P. a. occidentalis* to be considered *P. a. atricapillus* because they look like the latter, when they arise as intergrades in an area geographically remote from *P. a. atricapillus.* But the situation in the juncos is different. Here the hybrids (comparable to the intergrades) have seemingly at one time produced a race. The use of the name for all *cismontanus*-like hybrids as well as for the true race is advocated as a practical measure. This does not apply to sporadic isolated hybrids on the breeding grounds. The Jasper Park slate-colored juncos may for convenience be called *cismontanus,* even though by themselves they could be thought of as hybrids, or perhaps intergrades, rather than as part of a definite race.

The gradual mergence of *cismontanus* with *hyemalis* in the Edmonton and southern Yukon areas has been indicated. The intergradation does not consist of intermediate differentiation, but is a diffusion by interbreeding of characters of *cismontanus* (the *oreganus* elements) northeastward through continuous populations until such characters to all purposes disappear in pure *hyemalis.*

A summary of information useful to the taxonomist follows.

Junco hyemalis cismontanus

Racial characters.—*Cismontanus* is differentiated from *J. h. hyemalis* by extension posteriorly of dark area of pileum to a definite neck line in 80 to 95 per cent. Head averages darker, in males 6.1–6.4, instead of 7. Back rarely *a* or *b,* usually *aa* and *aaa* as in *J. h. hyemalis,* but about one-third to one-half have type 3 phaeomelanin even in advanced plumages. Females seldom entirely gray on sides. In both sexes sides frequently set off from hood, even though gray. No useful differences in size and tail markings exist.

Cismontanus differs from *J. o. montanus* in the presence of pure gray or slate sides in males or in gray or partly gray sides anteriorly in females (80 to 85 per cent). Head averages lighter; males 6.1–6.4 instead of 4.0. Contrast of head and back less pronounced, though distinct. Back darker in 95 per cent of males; *hyemalis* backs of retarded type (females) and *montanus* backs often identical. A male by reason of the presence of at least some gray in the sides together with other *hyemalis*-like features is never to be confused with pure *montanus.* Tail markings similar. Toes average 2 per cent longer.

Cismontanus differs from *J. o. oreganus* in the same way as from *montanus.* Additionally, there is a greater contrast in head color, and the back of *cismontanus,* which never is brighter than type 3, is never to be confused with types *oo* or *ooo* of *oreganus. Cismontanus* averages 5 per cent longer in wing and tail, 1 per cent shorter in tarsus and toes. Tail white on the average is much more extensive on rectrices 4 and 5.

Nongeographical variation (see also pp. 329–341).—Averages for the Stikine and Atlin groups correspond closely, except for those for bill depth, thus making possible, with the one exception, the combination of the groups for statistical treatment. Wing and tail are about 1 per cent longer than in *hyemalis* (Alaska and Mackenzie). The difference, though slight, is probably reliable statistically. Thus *cismontanus* surpasses slightly its presumed parents, northern *montanus* and *J. h. hyemalis.* Certainly there is no evidence from measurements that the short-winged *J. o. oreganus* was involved in the origin of *cismontanus.* Bill length is similar to the parental types, which are nearly identical. Bill depth in the Atlin group averages about the same as in *hyemalis,* the averages for females being a little higher; the Stikine group averages about the same as in northern *montanus.* This curious difference between groups that otherwise appear to be essentially the same stock emphasizes the possibility of separate but comparable derivation in which one group retained the deep *hyemalis*-like bill and the other the shallow bill of northern *montanus.* Foot measurements agree closely with those of *hyemalis.*

TABLE 34

MEASUREMENTS OF J. H. CISMONTANUS

(Populations from Atlin and interior Stikine River regions)

Measurement	Sex	No. of specimens	Mean with prob. error	Standard deviation	Coeff. of var.
Wing..............	♂	46	79.08 ± .18	1.88	2.37
	♀	40	74.33 ± .19	1.80	2.42
Tail..............	♂	44	70.09 ± .22	2.17	3.09
	♀	38	65.45 ± .20	1.82	2.78
Bill...............	♂	34	8.11 ± .03	0.29	3.67
	♀	32	8.10 ± .05	0.39	4.77
Tarsus............	♂	51	20.43 ± .04	0.45	2.21
	♀	40	20.25 ± .06	0.53	2.59
Middle toe.........	♂	51	11.74 ± .04	0.39	3.40
	♀	40	11.51 ± .04	0.37	3.20
Hind toe...........	♂	51	8.22 ± .03	0.34	4.20
	♀	40	8.05 ± .04	0.40	4.92
Bill depth (Atlin)...	♂	19	6.02	—	—
	♀	17	6.03	—	—
Bill depth (Stikine)	♂	17	5.78	—	—
	♀	13	5.70	—	—

Coefficients of variability compare closely with those of *hyemalis.* There is no increased variability. Again, as in populations of immediate hybrid origin, increased variation in size characters is not manifest.

Coefficients of correlation are: wing and tail, .762 ± .043; wing and tarsus, .375 ± .085; middle toe and hind toe, .360 ± .083. The last two of these correlations are somewhat doubtful because of the large probable errors. Sexual dimorphism of wing and tail is 6 per cent. It is absent in the bill. Slight dimorphism (1 to 2 per cent) occurs in the feet. The dimorphism of wing and tail is comparable to that in the parent races; that of middle toe and tarsus is like that in *hyemalis;* dimorphism in bill depth also is absent in *montanus.*

The difference in the hind toe may not have significance, but it is like that found in *montanus.*

Tail patterns are of exactly the same types as found in *J. h. hyemalis* and the average occurrence of types is essentially identical (see table, p. 317). There are no significant differences in *montanus, cismontanus,* and *hyemalis* pattern. The absence of any tendency in *cismontanus* to show reduction of white is important as further evidence that *J. o. oreganus,* with its reduced tail white, was not concerned in its origin.

Distribution in breeding season.—Occurs from extreme south-central Yukon Territory (Carcross) south through interior British Columbia east of the coast ranges into the interior Stikine River basin. The eastern limits in the northern Cassiar district are not known; probably the race extends eastward into the headwaters of the Dease and Liard rivers. South of the Stikine region it occurs east of the continental divide in the upper Peace River drainage south to Jasper Park. (For detailed occurrence of hybrids and of populations of *cismontanus* see foregoing discussions, pp. 333–341.)

Distribution in winter.—The impossibility of distinguishing hybrids of *hyemalis* and *oreganus* from the stabilized hybrid race *cismontanus* precludes accurate definition of the wintering range of the latter. The following account covers the distribution of "*cismontanus*-like" birds, hybrids included.

Winters most commonly in the southern Rocky Mountain region, together with *montanus* and *hyemalis,* and with fair regularity in California. In the north, winter-taken specimens of certain identity are known from southern British Columbia (Sumas); Minnesota (Minneapolis, Lanesboro); Wisconsin (Beaver Dam, Milton); Michigan (Ann Arbor); and eastern New York (Hastings). Southern records are from Lower California (Laguna Hanson), southern Arizona, and New Mexico (many localities), and Texas to Kendall and Kerr counties in the San Antonio district. There are records from Oklahoma, Arkansas (Van Buren, Delight, Winslow), Missouri (Shannon County), Illinois, and Indiana in a southeasterly direction. East of the Mississippi, *cismontanus* is rare and even in Kansas it constitutes but a small fraction of the wintering juncos. Records of occurrence on the eastern seaboard are for the most part doubtful, the birds probably representing variants of *hyemalis* (Massachusetts, New York, District of Columbia). A bird from Vanceville, North Carolina, seems indistinguishable from this race. There is some question, however, of whether it actually arose in the breeding area of *cismontanus.* Yet banding records reported by Lincoln (1933, p. 338) show that juncos (*J. h. hyemalis ?*) may move eastward from Minnesota to New Jersey, and from North Dakota to Pennsylvania. On the Pacific coast, *cismontanus* occurs rarely in western Oregon and Washington. In California, records for the coastal districts are chiefly from localities south of the northern humid coast belt.

Junco aikeni

White-winged Junco

This strongly marked member of the *hyemalis* artenkreis is geographically one of the most isolated species occurring on the continent north of Mexico.

Not only is the breeding range in the Black Hills district of the plains region of small extent, but the true wintering range is small and well defined. There are almost no instances of migration out of the plains and Rocky Mountain regions that are based on critically determined specimens.

Principal characters of the species.—Sides fairly pure light gray (deep to light mouse gray); the color may be obscured somewhat by drab and smoke gray tipping. Ventral hood margin concave posteriorly owing to confluency of gray of sides and breast. Lores and ocular region not distinctly darker than rest of head. Back area indistinctly differentiated from head and of same color when drab streaks and tipping are absent. In advanced plumages dorsum clear light gray, same as ventral surface of hood. Arrangement of pigments in feathers as in *J. hyemalis* (see p. 313).

Middle and greater wing coverts usually with some white. Tail with three outer tail feathers largely white, and white usually present on third rectrix. Dimensions distinctly large throughout. Wing and tail longer than in any other junco (some overlapping); bill tumid, about as large as in *alticola;* feet relatively small, only slightly larger than in *J. h. hyemalis* and *J. o. oreganus.* Weight of males (average of 19) 22.0 gr. Iris brown; bill and feet flesh color.

Differential characters.—*Aikeni* differs from *J. h. hyemalis* in its lighter slate, almost ashy dorsal coloration; only in decidedly retarded plumages might there be confusion of the two forms. *Aikeni* usually has white spots on middle and greater secondary coverts; when these are absent, margins of feathers light gray, unlike *J. h. hyemalis;* white spots occur in 3 per cent of *hyemalis.* White on third rectrix occurs in 94 per cent of *aikeni,* 2 per cent of *J. h. hyemalis.* Bill heavier, usually somewhat tumid basally, and culmen not so distinctly ridged. Wing averages 12 to 13 per cent longer; tail, 15 to 16 per cent longer; bill, 9 to 11 per cent longer; bill depth, 20 per cent greater; tarsus, 2 to 3 per cent longer; middle toe, 2 per cent longer.

There is essentially no overlapping in measurements of wing, tail and bill depth. The absolute minimum (1 out of 50) of *aikeni* may be equaled by the maximum (1 out of 100 or more) of *hyemalis.* Wing length of 82 mm. or greater, tail of 75 or greater, and bill depth of 6.8 or greater in males may be taken as reliable diagnostic measurements of *aikeni.* Comparable minima of females are: wing, 79; tail, 72; bill depth, 6.6.

In spite of the approach of *J. h. hyemalis* and *aikeni* in all the essential points of difference, the absence of any consequential overlap in a large number of characters precludes the possibility of confusion of the two forms when all of them are considered. I have yet to examine an equivocal specimen, so far as these two forms are concerned. Their status as distinct species seems entirely satisfactory.

Aikeni differs from *mearnsi,* its nearest neighbor in the breeding season, in size to nearly the same degree that it does from *hyemalis.* In coloration it differs in the same way that the entire artenkreis of slate-colored juncos differ (see p. 314) from *mearnsi* and the other Oregon juncos. There is no approach in side coloration (slate or gray, as against pinkish cinnamon) or in the color and demarcation of the back (slate or buffish slate as against brown, definitely delimited anteriorly from the head). *Mearnsi* does have white in the third rectrix in 17 per cent of males (94 in *aikeni*) and occasional white spots on the secondary coverts (1.82 per cent).

Nongeographical variation.—The amount of white present on the wing is exceedingly variable. The percentage of occurrence of pure white areas on different groups of feathers is:

Sex	No. of specimens examined	No white	White on middle coverts but not on greater coverts	White on middle and greater coverts	White on inner secondaries
♂	86	5	4	91	22
♀	134	22	8	70	2

No account is taken in the foregoing tabulation of the number of feathers in each series marked with white. On the inner secondaries the amount of white is highly variable. Usually it is confined to the tips and inner webs of the three innermost secondaries (so-called tertials), but it may extend to five or six of the secondaries and on some it occupies a terminal area that extends 3 or 4 millimeters along the vane. The pronounced sexual difference is similar to the condition in *hyemalis* (see p. 315). Association of larger amounts of white with the advanced plumages of the male does not support the suggestion that the wing bars of *aikeni* are a primitive character. The obviously immature birds of both sexes most often have inconspicuous white areas. The areas are, however, the same in position and outline as the buff wing spots of juveniles of all juncos. Juvenal *aikeni* may not have pure white spots, but they average whiter than in other species. The best view concerning this character in *aikeni* is, then, that a juvenal, presumably archaic, feature has been accentuated to some degree in this species.

Variations in the amount of suffusion of the light slate with buff are much less pronounced than in *hyemalis*. The gray of the sides is never fully replaced or obscured by buff. The relation of retarded plumage to sex and age is comparable to that in other slate-colored juncos, particularly to that in *J. h. carolinensis*. Variation of the gray or slate of the head ranges in males from types 8 to 10, chiefly 9, and in females from 10 to 11.

All variants involving white on the first and second rectrices are peculiar to the species *aikeni*. (There is one *mearnsi* with a white spot on the second rectrix.) Likewise, mixed white, predominantly white and pure white patterns on the third rectrix are peculiar to *aikeni*. Absence of pure black fourth rectrices, of black and mixed black fifth rectrices, and of impure white sixth rectrices are departures from *J. h. hyemalis* in accord with the general trend of increased whiteness. There is no other junco except *vulcani* so strongly set off from adjacent forms in amount of tail white. Sexual dimorphism as usual is present in all feathers that show appreciable variation in pattern (rectrices 3, 4, and 5). The sexual dimorphism is much greater than in *J. h. hyemalis*, in which, abnormally for the genus, it is almost lacking.

The coefficients of variability are relatively high, compared with those of *J.*

TABLE 35

Occurrence of Rectrix Pattern in J. aikeni and J. h. hyemalis (in Percentages)

	Males		Females	
	aikeni	*J. h. hyemalis*	*aikeni*	*J. h. hyemalis*
Rectrix 1 (innermost)				
Inner web:				
trace of white	0	0	3	0
Rectrix 2				
Inner web:				
trace of white	22	0	8	0
Outer web:				
trace of white	6	0	3	0
Rectrix 3				
Inner web:				
pure black	6	98	8	100
trace of white	29	2	64	0
mixed	57	0	22	0
trace of black	6	0	6	0
pure white	2	0	0	0
Outer web:				
pure black	27	98	50	100
trace of white	8	2	19	0
mixed	37	0	25	0
trace of black	20	0	6	0
pure white	8	0	0	0
Rectrix 4				
Inner web:				
pure black	0	16	0	22
trace of white	0	50	3	48
mixed	2	34	14	30
trace of black	16	0	31	0
pure white	82	0	52	0
Outer web:				
pure black	0	54	0	48
trace of white	0	10	2	26
mixed	25	20	50	13
trace of black	12	12	17	9
pure white	63	4	31	4
Rectrix 5				
Inner web:				
mixed	0	14	0	39
trace of black	2	18	0	13
pure white	98	68	100	48
Outer web:				
trace of white	0	0	0	4
mixed	0	36	0	35
trace of black	6	20	6	13
pure white	94	44	94	38
Rectrix 6				
Inner web:				
pure white	100	100	100	96
Outer web:				
pure white	100	100	100	96

hyemalis and *J. oreganus*. Wing length is as highly variable as in any other species of the genus (equivalent to *alticola*). The tail reflects none of this great variability. Bill length is slightly less variable and bill depth is much less variable than in *hyemalis*. The hind toe is more variable. In such a restricted form it is indeed interesting to find instances of high variability. The relative uniformity of bill is important in a form where this member is of such distinctive size.

Correlations are as follows: wing and tail, .758 ± .041; wing and bill length, .552 ± .066; wing and tarsus, .317 ± .088; tail and bill length, .411 ± .079; tail and tarsus, .280 ± .088; bill length and tarsus, .516 ± .072; bill length and bill depth, .281 ± .088; tarsus and middle toe, .415 ± .081. The correlations above .4 certainly are significant, as also probably all those here listed. Other correlations are below .25. A common correlation of wing, tail, bill, and tarsus suggests that there are some general factors for size in this giant species. In *hyemalis* only wing and tail were correlated and, separately, the parts of the foot. In *carolinensis,* which is somewhat larger than *hyemalis,* extensive correlations exist that are similar to those of *aikeni,* except that bill depth rather than bill length is concerned. The situations are therefore comparable but not identical. In *carolinensis* bill and bill depth are correlated at .364; in *aikeni* the correlation is .281; there is no correlation in *hyemalis*. As in other systems of correlated parts, it appears that certain common factors are present but that such factors are not equally important in determining the adult size in the several parts. Each part has its own independent set of controls. Certainly bill depth, so distinctive in *aikeni,* must have a set of factors not associated with other size characters. Possibly some of these affect bill length, or are linked with those that do. Middle toe and tarsus are correlated as usual, but hind toe definitely is not; perhaps significant in this connection is the fact that the hind toe is no larger than that in other northern juncos. Middle toe is not

TABLE 36

MEASUREMENTS OF JUNCO AIKENI

Measurement	Sex	No. of specimens	Mean with prob. error	Standard deviation	Coeff. of var.
Wing..............	♂	50	87.80 ± .27	2.81	3.19
	♀	38	83.08 ± .26	2.36	2.84
Tail..............	♂	50	79.60 ± .23	2.51	3.14
	♀	35	76 61 ± .28	2.51	3.27
Bill..............	♂	50	8.89 ± .03	0.31	3.51
	♀	35	8.76 ± .04	0.34	3.91
Bill depth..........	♂	49	7.17 ± .03	0.27	3.82
	♀	35	7.16 ± .03	0.28	3.97
Tarsus............	♂	50	21.13 ± .05	0.55	2.59
	♀	36	20.76 ± .07	0.66	3.21
Middle toe.........	♂	47	11 89 ± .05	0.52	4.39
	♀	37	11 62 ± .06	0.55	4.69
Hind toe...........	♂	47	8 44 ± .05	0.52	6.15
	♀	36	8.11 ± .05	0.41	5.03

correlated with wing, tail, or bill, so that its association with the tarsus rests on different factors than the general size factors that have been hypothesized.

Significant sexual dimorphism is as follows: wing, 5 per cent; tail, 4; tarsus, 2; hind toe, 4. This situation differs from that in *hyemalis* in the lesser dimorphism in wing and tail and in the absence of significant differences in the bill. Difference in wing and tail in *aikeni* is 10 per cent in males, 9 per cent in females. Both figures are lower than in *hyemalis* and equal to those in the nonmigratory *carolinensis*.

Distribution in the breeding season.—Breeds in the Black Hills of South Dakota and in similarly pine-forested areas in southeastern Montana, northeastern Wyoming, and northwestern Nebraska. The regions lie chiefly within areas mapped by Cary (1917) as Canadian Zone, but some are Transition in character (Saunders, 1921, p. 13). Forests are relatively arid, with yellow pine (*Pinus ponderosa scopulorum*) dominant. Second-growth pine forests and pine forests mixed with scrubby growth of oaks may be inhabited. The forests lie in regions that receive from 15 to 25 inches of rainfall annually. This environment is comparable to that in the lower arid regions of the breeding ranges of *caniceps* and *mearnsi*. Altitudinal range is from below 4000 (Long Pine Hills, Montana) to 7200 feet. (See fig. 9.)

Montana.—Known to breed in the Long Pine Hills of Carter County (Visher, 1911, p. 14) and in western Powder River County near Otter. Birds taken in April at Miles City, Custer County (Saunders, 1921, p. 124), probably were not on their breeding grounds. Professor Joseph Kittredge (MS) reports seeing the species in May in the forests of Powder River County, south of Stacey. Probably occurs in essentially unmixed populations in various of the pine hills in Fallon, Powder River, Rosebud and eastern Big Horn counties.

Wyoming.—Breeds in the Bear Lodge Mountains (Warren Peaks), in the vicinity of Sundance, and in the Black Hills of eastern Crook and Weston counties; possibly also in extreme eastern Niobrara County.

South Dakota.—Black Hills of Lawrence, and western Meade, Pennington, and Custer counties. Probably occurs also in hills of Harding County.

Nebraska.—Breeds in northern Sioux County and probably also in pine areas at the headwaters of the White River in Dawes County.

The record of breeding in Colorado (Cary, 1909, p. 182) is not substantiated by specimens. It is extremely unlikely that *aikeni* nests in that state. I have examined a specimen taken June 26, 1917, at Alice, Clear Creek County, by R. S. Niedrach. There is no certainty that this bird was breeding; it was probably a retarded migrant. Tate's record of the breeding of *aikeni* in Cimarron County, Oklahoma, needs further confirmation. The region is one that does not appear to offer suitable breeding habitat, even though a spur of the Rocky Mountains extends eastward at this point, bringing with it scattered low-zone coniferous trees. If juncos should breed there, the probability is great that they would prove to be *caniceps* rather than *aikeni*, because the former occurs about 100 miles west of this point. The nearest proven breeding grounds of *aikeni* are 600 miles to the northward.

Distribution in winter (November 1 to March 15).—Remains in the vicinity of breeding areas as at the Long Pine Hills, Montana (Saunders, p. 124), Hat Creek and Newcastle, eastern Wyoming, and Crawford, Nebraska. Also migrates southward to winter along eastern slopes of the Rocky Mountains and the western part of the plains as far as Oklahoma (Fort Reno) and New Mexico (Las Vegas and vicinity of Santa Fe). Probably occurs in northern Texas. Occasional in Arizona in the vicinity of Flagstaff and in the White Mountains in 1937 (Hargrave, Phillips, and Jenks, 1937, p. 258).

The majority of known specimens are from the bases of the mountains in central and northern Colorado. Birds have been examined from Wallace and Morton counties, Kansas. There is little reason to doubt that the record (Cooke) from Ellis, Ellis County, pertains to this species, but supposed *aikeni* from eastern Kansas that I have examined have proved to be *J. h. hyemalis.* Cooke's record from Caddo, Bryan County, southern Oklahoma, is based on a skin; he presents additional sight records. The specimen has not been available to me, but his statement that two of the tail feathers are all white, and a third partly so, leads me to suspect that the bird was not *aikeni.* His record for Wisconsin is likewise to be doubted, for he states that the specimen was exactly like the one from Caddo. It is entirely possible that *aikeni* ranges east of the vicinity of Oklahoma City, for there are several sight records east as far as Tulsa, but, as in eastern Kansas, it would seem best that specimens critically compared with *aikeni* with regard to all characters be at hand before definite conclusions are drawn.

Relationships with other species. J. o. mearnsi.—Evidence of hybridization of these species was first found in a single specimen from the University of Colorado collection at Boulder. This bird, a male, no. 99 of Dille, the collector, was taken at Altona, Boulder County, February 6, 1902. Of a number of supposed hybrids taken in winter, this is the only one that is not merely a *mearnsi* with the white wing spots which may be considered a "normal" variation of that species. Dille's specimen is certainly a hybrid. The head is about type 9, which is an intensity of color common to the two species. The coloration of the back is *mearnsi* but the back is not very sharply set off from the head. The hood line below is concave as in *aikeni.* The sides are mixed bright pinkish cinnamon (*mearnsi*) and light gray (*aikeni*). The manner of mixing is comparable to that found in *J. o. montanus–J. h. cismontanus* hybrids or in *J. c. caniceps* × *J. o. mearnsi.* There is no trace of white on the wing coverts, but gray edgings are prominent. Wing and tail measurements fall between the averages of the two forms, at a point about equal to the minimum of one species and the maximum of the other. The bill is large, but it is closer to that of *mearnsi* than that of *aikeni;* it is not so distinctly tumid as in *aikeni.* White on the tail extends to the third rectrix as it does occasionally in *mearnsi* and nearly always in *aikeni.* The amount of black on rectrices 4 and 5 is greater than in *aikeni.*

The only alternative to considering this bird a hybrid of *mearnsi* and *aikeni* would be to look upon it as a hybrid of *mearnsi* and *hyemalis.* But all the *hyemalis* elements in it could equally well have come from *aikeni.* Besides, the wing and tail length could never have been derived from *hyemalis,* and there is little chance that the light gray in the sides would have come from that source.

Subsequent to the study of this bird a field party from the Museum of Vertebrate Zoölogy visited a forest area in western Powder River County, Montana, which seemed the most likely point of origin of such a winter-taken hybrid. At 4 miles west of Fort Howe Ranger Station a breeding sample of 30 adult juncos, with 9 juveniles, was taken. The population was dominantly *aikeni*. Only 3 birds showed evidence of *mearnsi* blood, but this evidence was conclusive.

Apart from these 3, the *aikeni* population seemed essentially typical. Average measurements except for bill length were a little lower than in the main sample of winter-taken *aikeni* from Colorado that form the basis of the tables presented for this species. Most of the differences are not reliable statistically and even if valid may well represent a faint colonial differentiation independent of *mearnsi* influence. This seems all the more likely because the amount of tail white in the sample is prevailingly a little greater than in other *aikeni*, a trend opposite from that which would result from *mearnsi* mixture. As regards white on the wing, a larger percentage (♂ 16, ♀ 33) than normal were without it, but also a larger percentage (♂ 50, ♀ 22) had extreme development of white that extended to the inner secondaries. The color of the hood is apparently normal for breeding *aikeni*, although it might prove to be a little darker than normal if a large breeding series from the Black Hills were compared.

The 3 hybrids from this population, 2 males and a female, were all in full breeding condition. The nature of the mates of none of them is known. One male (no. 7328 W. C. Russell) is in most respects *mearnsi*. The head is type 8. The back is brown as in *mearnsi* on many of the distal parts of the feather vanes, but unlike the coloring in *mearnsi* there is much of each feather that is slaty. The mass effect is one of intermediacy. I have seen no *mearnsi* in which the back is anything but pure brown. The hood line is convex as in the *oreganus* group and the sides are pure pinkish cinnamon, although the area of color is narrower than normal for *mearnsi*. Wing is near maximum for *mearnsi* and minimum for *aikeni*; tail is below average for *mearnsi*; bill length is almost average for *aikeni*, but bill depth is minimum for *aikeni* and maximum for *mearnsi*. White in the tail extends inward to the third rectrix, but the black on rectrix 4 is more than in males of *aikeni*. There is no white in the wings.

The second hybrid male (no. 1025 F. H. Test) is chiefly *aikeni* in character. The head is type 9 and the back without trace of brown. The hood line is, however, convex as in *mearnsi*. The sides are not pinkish cinnamon, but are smoke gray and pale slate so that they contrast with the hood. Wing and tail are minimum and average for *aikeni*, respectively; bill measurements are above average for *aikeni*, approaching maximum. Tail white is normal for *aikeni*. There is no white in the wing.

The female (no. 7325 W. C. Russell) is decidedly mixed in character. The head is type 9 and the back is without trace of brown. The hood is convex and the sides are mixed light slate and bright pinkish cinnamon, the former predominating. The wing has white spots on the middle coverts, larger than in the variants that occur normally in *mearnsi*. Wing and tail are above average for *aikeni*; bill measurements are near maximum for *aikeni*. The white of the tail extends inward to the second rectrix, a coloration detail that is never found in female *mearnsi.*

These 3 hybrids from the breeding range of *aikeni* prove that occasional *mearnsi* wander eastward from their breeding range in the Big Horn Mountains of Montana and Wyoming to breed with *aikeni.* The rarity of such hybrids in the large wintering flocks of Colorado would indicate that hybridization of the two is rare indeed. *Mearnsi* and *caniceps* hybrids are encountered with fair regularity, whereas their breeding ranges are but little more closely connected than those of *mearnsi* and *aikeni.* Between the Fort Howe area and the Big Horn Mountains there are scattered areas of yellow pine forest. The greatest interval between junco habitats is probably no more than 20 miles and probably much less, and the total interval is about 70 miles. In view of this fact it is remarkable that more hybridization does not occur, although it is granted that populations of more mixed character than now known may be found in Rosebud and eastern Big Horn counties. Here are two forms, each representative of an extreme modification of a distinct rassenkreis, that remain peculiarly apart, considering their migratory habit, when in close proximity geographically in the breeding season. They must have had a long history of divergent evolution. Through some factors of habitat preference and specific intolerance, or both, they remain essentially separate, as do species rather than races. This is all the more remarkable in view of their physiological capability of hybridization. The ability to hybridize becomes particularly dubious as a sole criterion of specific distinction when situations like this are encountered.

The breeding ranges of *aikeni* and *hyemalis* are separated by at least 500 miles of uninhabited territory. One may suspect that during glacial periods *hyemalis* was forced southward in the breeding season, possibly once to the vicinity of South Dakota. The Black Hills remained free of glaciation in the Pleistocene. *Aikeni* may then have been a local southern race of *hyemalis,* as *carolinensis* is today. Many of its characters correspond to modifications in other forms in arid regions. Its large size and pale color parallel, and even surpass, *carolinensis.* Subsequent isolation with the retreat of northern populations could have aided in the preservation and propagation of new variants within it.

Alternative views concerning origin cannot be overlooked. *Aikeni* might represent an archaic remnant of the original *hyemalis* stock. But the large amount of white in the tail is far from primitive, viewing the genus as a whole. This and the accentuated juvenal wing bars appear to correspond with the prevailing arid environment. An ancestral junco might be expected to be of a size more like that of the average of the genus, not a giant form. *Aikeni* may have been pre-Pleistocene in origin, dating back to the arid period in the plains in the Pliocene. In any event, it resembles a geographic race, although it is now fully dissociated from its one-time racial relatives as a species. It is not clearly a primitive form in the sense that *vulcani* may be so considered. It may well have diverged contemporaneously with *hyemalis* from a common stock, each retaining unmodified certain of the original characters of that stock.

DISCUSSION AND SUMMARY

INTRARACIAL CORRELATIONS

The most striking series of correlations has to do with wing and tail length. In no race is correlation of these two absent, but it may differ greatly in value (see graph, fig. 32). Two explanations for the association of wing and tail length have been offered. The first is that the same series of factors determines the growth of the similar major feathers of wing and tail. These determiners might be effective in controlling size of body as a whole and might control wing and tail length only incidentally. Therefore, the net correlation of wing and tail additional to the correlation of each with body size should be known. This relation is difficult to determine, because there is not much information that can be obtained from the material at hand to indicate body size. Lengths of skins mean nothing. Weights are the most useful measure and are more constant than is usually supposed (see p. 254). In one race (*montanus*), in which an adequate number of weights is available, the net correlation of wing and tail is .623, whereas the gross correlation is .646; the coefficient for wing and tarsus is .237. Tarsus is not correlated with wing and tail to a significant degree, except in a few races. We can conclude, then, that wing and tail correlations are in large measure independent of body size.

The second explanation of correlation rests on the linkage of factors that might independently affect wing and tail. It is assumed from study of naturally occurring hybrids that wing and tail lengths are governed by multiple factors (see p. 195); this is in no sense to be considered as proved. Multiple factors, that could be distributed in a number of chromosomes, would have little chance of being so linked as to effect a fairly constant and close association of a given wing and tail length. Especially is it unlikely that such a linkage system would hold in a number of distantly related forms where new factors must come into the complex (perhaps, however, only as multiple allelomorphs) to produce different wing and tail lengths characteristic of these forms. There is little likelihood, therefore, that genetic linkage is the cause of correlation.

The variation in wing and tail that is not correlated, although partly somatic, must to some degree be determined by factors that affect these parts independently. If such specific factors did not exist, it would be difficult to explain the difference in wing and tail ratio in two closely related races, each of which possesses an equivalent coefficient of correlation of wing and tail. Further evidence along the same line is found in the fact that some races show an increased coefficient of variability in the tail while there is a decreased variation in the wing, or vice versa (see graph, fig. 32). In general, where there is a close correspondence in the coefficients of variability of wing and tail, these parts tend to be more highly correlated, and where variability is distinctly different, the correlation drops. Thus, in the latter situation it is supposed that some new factors have appeared to control independently one or the other member. Associated with this, there is often a difference in absolute value of wing or tail length as compared to that of the most nearly related races. The consistently higher variation of the tail is most probably due to somatic variation, although there may be more independent factors concerned with this member.

Consideration of the foregoing factors indicates a mechanism of variation which shapes the result of selection pressure and mutation pressure and which doubtless has been important in the origin of the characteristic average dimensions of the races as they exist today. In summary, this mechanism would seem to consist of (1) a set of multiple factors which to a high degree determines the lengths of both remiges and rectrices, (2) factors for general body size, which have only a very slight control over length of the feathers, (3) some factors which may control wing or tail independently, or at least disturb the balance of the two, and which effect alterations in relative length. and (4) somatic variation. Theories concerning the trends in evolution of wing and tail length and the method of such evolution should take into account this fundamental system of control.

No other intraracial correlations of large magnitude run through all forms of juncos with a constancy approaching that of the wing and tail. Bill and bill depth in a few scattered instances are correlated. These two dimensions depend on somewhat independent growth processes. Both would of course reflect a general massiveness of bill, but the length depends partly on growth of the horn structure terminally, whereas the depth depends on the size of the bones and to some degree the massiveness of the whole head. The only juncos that display significant correlations are the relatively large-billed forms, *vulcani, carolinensis, aikeni,* and *insularis,* with coefficients of .599 ± .192, .364 ± .067, .281 ± .088, and .261 ± .066, respectively. Other distinctly large-billed types, *alticola* and *dorsalis,* do not show this. In each of the forms showing correlation the bill is larger, to varying degrees, than in the forms which obviously are most nearly related. One is tempted to suppose that the new factors responsible for larger bill are those that act on both bill length and depth. Sometimes they may be general size factors, for there is some correlation of a great many parts in these forms, excepting *insularis.* But because weights are not available, this cannot be proved. In *insularis,* the correlation clearly is confined to the bill, and the species obviously is a small form. The factors responsible for its strikingly great bill size would therefore seem to be partly factors that affect this member exclusively and cause some measure of correlation in the two bill dimensions.

Bill length is correlated with both wing and tail in *vulcani* and *aikeni,* and slightly so in *carolinensis.* Bill depth is correlated with wing in *carolinensis* and *vulcani,* but not in *aikeni.* Despite this latter exception, this evidence supports the idea of common size factors in these forms. In the bill low correlations may be obscured by variations due to wear and to displacement of the mandibles in the course of preparation of the skins. These factors are partly responsible for the prevalently high coefficients of variability.

In a different category are the correlations of wing and bill depth in *alticola* (.434 ± .08), *bairdi* (.240 ± .08), and *mearnsi* (.427 ± .07). In these forms there is no widespread correlation of parts and none of significance of bill and bill depth or of bill length and wing. *Bairdi* and *mearnsi,* at least, are not importantly different from closely related forms in absolute value of bill depth. These correlations suggest to me linkage, which of course must mean either that there are different factors involved with different loci, compared with related forms, or that some translocation of parts of chromosomes has occurred to establish close linkage of the factors.

To summarize, bill length and depth are not often correlated, and if they are, the coefficients usually are not high. In a few instances general size factors would seem to play a part in bringing about correlation. In one race common factors for bill and bill depth are suggested. Otherwise the determination of the two bill dimensions is more or less independent, but bill depth occasionally shows strong association with wing length (probably wing and tail), an association which suggests a linkage phenomenon. Judging from what now exists, variations and associations of several kinds may appear with respect to the bill, thus leaving the way open for evolution in bill proportion of any sort and degree, and for change in general size of bill with or without corresponding modification in other parts.

Tarsal and toe length would seem to be determined by a number of factors. The usual picture of quantitative inheritance is shown in such natural hybridizations as have been studied. The correlation of foot parts seldom reaches .5. Usually it is .2 or .3, or lower, so that its significance is doubtful in small samples. Correlation of foot parts is erratic in the genus as a whole. Some forms show correlation of tarsus and middle toe only, others of tarsus and hind toe only. The correlation is always slightly positive, but it may be no larger than the probable error. In those forms which have general systems of correlation it is not always present. It seems to be quite absent in *vulcani,* for example. Many of the relatively large-footed forms, such as *alticola, insularis,* and *J. o. oreganus,* show much correlation, but others do not, notably *vulcani.* The indices for variability in toe length run high. More than with the wing, errors in measurement enter in that partly account for the high variability and that tend to obscure correlations of low or moderate magnitude.

Probably there are some general size factors that affect the feet to a small degree. Additionally there probably are some races with linked factors, or common factors, operative only on the foot, that have some effect. But there is almost always much independent variation of the parts concerned, which, if it is in any great measure hereditary, must be controlled in each instance by separate factors.

Correlations of characteristics other than those of dimensions have not been investigated extensively. Often the difficulty of classifying color in the available material has hindered statistical treatment. Amount of white on separate rectrices (4 and 5) was found to be well correlated (.620 ± .06) in *thurberi.* Such an association probably is generally prevalent in the genus. Apparently, extent of the wing bars and tail white are correlated in *aikeni,* although this could not be determined quantitatively. The amount of white in the tail is not correlated with coloration in other parts of the plumage; that is, lighter-headed birds do not have more white in the tail, even though such characters may show parallel evolution in a series of races.

In *montanus,* it was found that eumelanin of the head and of the back were correlated (.427 ± .038). Most probably there is some interaction of the factors for this pigment in the two areas, so that when a critical degree of darkheadedness occurs the back is influenced, and contrarily, when the head is pale to an extreme degree no great intensity of pigment in the back is possible. In *J. o. oreganus* a comparable correlation is lacking, but there is some association of dark head with intensity of phaeomelanin in the back. The color of the sides is not correlated with coloration of back or head in Oregon juncos, nor to any degree in *J. p. phaeonotus.* There seems to be no prevalent interrelation of different color areas. Parts of the body that are essentially monochromatic, like the head and sides in the *hyemalis* artenkreis and in *J. caniceps,* show correlation.

INTERRACIAL CORRELATION

It has been found in studies of geographic variation, for example by Sumner (1932, pp. 52–53), that characters that show correlative differentiation in a series of geographic forms may not be correlated among individuals of a given race. Presumably, selective factors have then been operative which have shaped the parallel modification of two features which are unrelated within the organism. Or else (Bubnoff, 1919, p. 166; Sumner, *loc. cit.*), the racial differences are genetic whereas the intraracial variation is nongenetic. Conversely, there are individually correlated characters which do not differentiate in races in any associated way. However, if two factors are associated because of common factorial control or related physiology of development, they might be expected in most instances to show some degree of parallel racial modification.

In the preceding section on intraracial correlation, it was brought out that the best example of prevalent association of characters is that of wing and tail length. The graph (fig. 29) demonstrates the interracial and interspecific correlation of these two. The parallelism is remarkable throughout, irrespective of whether the forms are weakly differentiated races or strikingly different species (*vulcani*). An increase in tail relative to wing is to be noted, especially in the yellow-eyed group of nonmigratory forms that ranges from Arizona southward. This is also seen in the southern members of the *hyemalis* and *oreganus* artenkreise. However, these independent alterations are insignificant in magnitude as compared with the correlated modification. The common genetic control of wing and tail must have had much to do with the correlative differentiation of the two in the genus.

Average weights for a few races (fig. 29) throw some light on general correlation of size of body parts. The wing and tail are but poorly correlated with weight, just as is true in intraracial variation. Complete reversal of the expected association of weight and length of wing and tail is seen in comparing *J. o. oreganus* and *J. o. montanus.* The small *bairdi* and *pinosus* are, however, short winged, and the giant *aikeni* is of course correspondingly long winged. Lack of correlation is very definite in *townsendi* and *montanus* and in *caniceps* and *palliatus.*

Tarsus correlates but slightly with wing and tail. Extreme differentiation in wing length is usually reflected in the tarsus, but not in equivalent degree (see the southernmost forms, fig. 29). A negative correlation is seen in the series of forms beginning with *dorsalis* and running through *J. p. phaeonotus,* and in *J. o. oreganus,* and, slightly, in *insularis.* Weights correlate with tarsus, and might, with more data, show a moderately strong correspondence throughout.

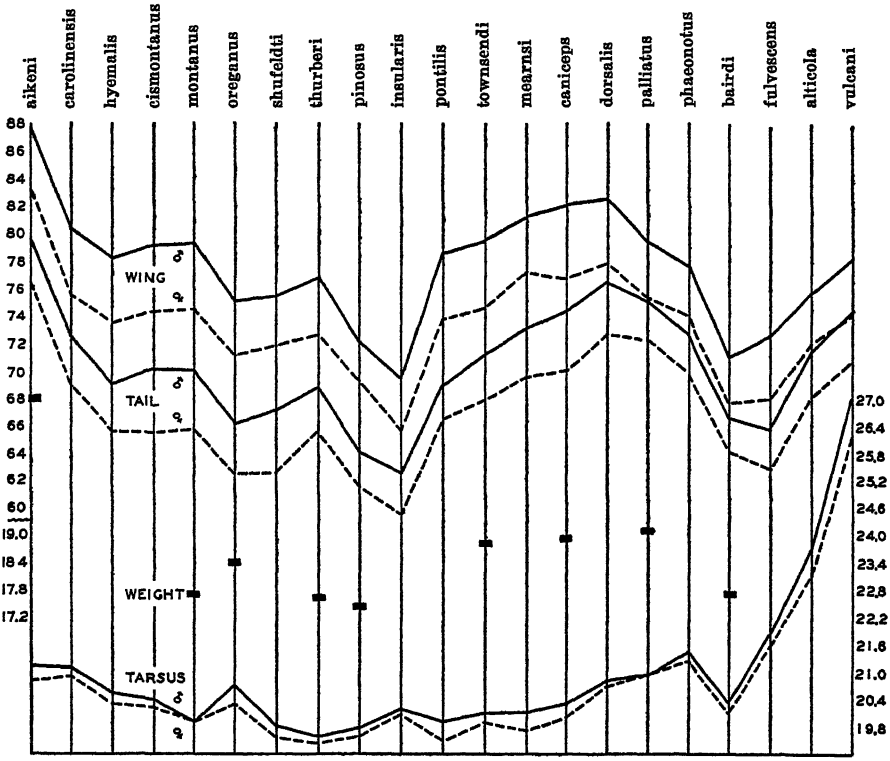

Fig. 29. Comparison of average wing, tail, and tarsal lengths in the 21 forms of the genus *Junco.* Measurements in millimeters: numbers at left for wing and tail; at right, for tarsus. Average weights in grams (numbers at lower left) for breeding males of certain races are shown by spots.

The middle and hind toes and the tarsus show a fair degree of correspondence throughout the genus (fig. 30). Only in magnitude of differentiation are there striking differences, as in *insularis.* Minor discrepancies in correlation are seen in comparing *aikeni* and *carolinensis,* and *palliatus* and *J. p. phaeonotus.* Modification must always preserve a functional balance, and hence radical changes in one part of the foot alone are not likely to appear.

Bill depth and length show some measure of correspondence, but there is a marked negative correlation of differentiation in the three southernmost forms (fig. 31). There is no prevalent correspondence of the bill with wing, tail, and foot. *Aikeni, alticola,* and *vulcani* are in a sense giant forms and accordingly have large bills, but this is most certainly not true of *insularis.* The bill, because of a usual lack of common factorial control of its dimensions and because there is no necessity for correspondence with body size for the sake of efficient action, becomes modified independently of other parts. Preservation of a certain balance of proportions within the bill may be expected even without developmental correlation, but even this can be, and is in some measure, broken down.

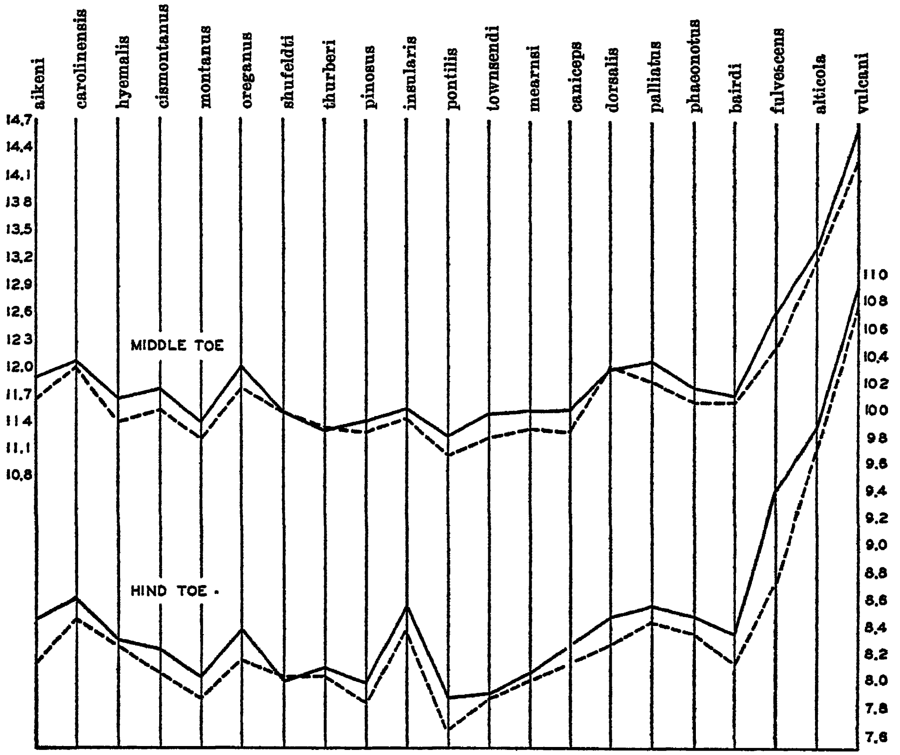

Fig. 30. Comparison of average middle-toe and hind-toe lengths in juncos. Measurements in millimeters: numbers at left for middle toe; at right for hind toe.

In tracing correlation of colors, forms should be considered according to geographic groups. Each rassenkreis or artenkreis may show its own system of interracial correlation, but between major groups there is so much difference in color because of long separate evolutionary history that correlation may be obscured. Color areas, when correlated, seem to correspond to some environmental factor that would appear to have a molding influence (probably indirect).

To exemplify, *J. hyemalis carolinensis* has a blacker head than *J. phaeonotus phaeonotus*, but it has a much whiter tail. But within the *phaeonotus* rassenkreis and within the *hyemalis* rassenkreis the correlation is quite clear. We might say that there is interracial correlation but not interspecific correlation. In measurements, both interspecific and interracial correlation occur, and they fit into one system.

It is difficult to represent the whiteness of the tail in simple fashion since the modifications of the pattern are complex. However, I have attempted to show in table 37 the gross differences in amounts of white.

It should be understood that tail white in *dorsalis* and *pinosus*, although roughly similar in amount, differs importantly in pattern. In *J. caniceps* and in the yellow-eyed groups the white is more widely distributed on several feathers (a primitive feature?), and less concentrated in large areas on a few rectrices. *Bairdi* and *insularis*, compared to each other and to their nearest relatives, have peculiarities in pattern. Using the seriation in the table, comparison with relative head color reveals the following associations. In the *hyemalis* artenkreis, head color and tail white correlate, *aikeni* being lightest and *hyemalis* and *cismontanus* darkest. *Cismontanus* possesses a distinctly darker head than *J. h. hyemalis,* yet its tail is no less white. Here another factor enters in, namely, the fairly recent derivation of the dark head of *cismontanus* by hybridization with *J. oreganus. J. h. hyemalis* and *J. o. montanus,* the presumptive parents, have the same amount of tail white. Further, there is no reasonable association of head color of *cismontanus* with conditions of aridity or moisture, as there is in *aikeni* and *carolinensis.*

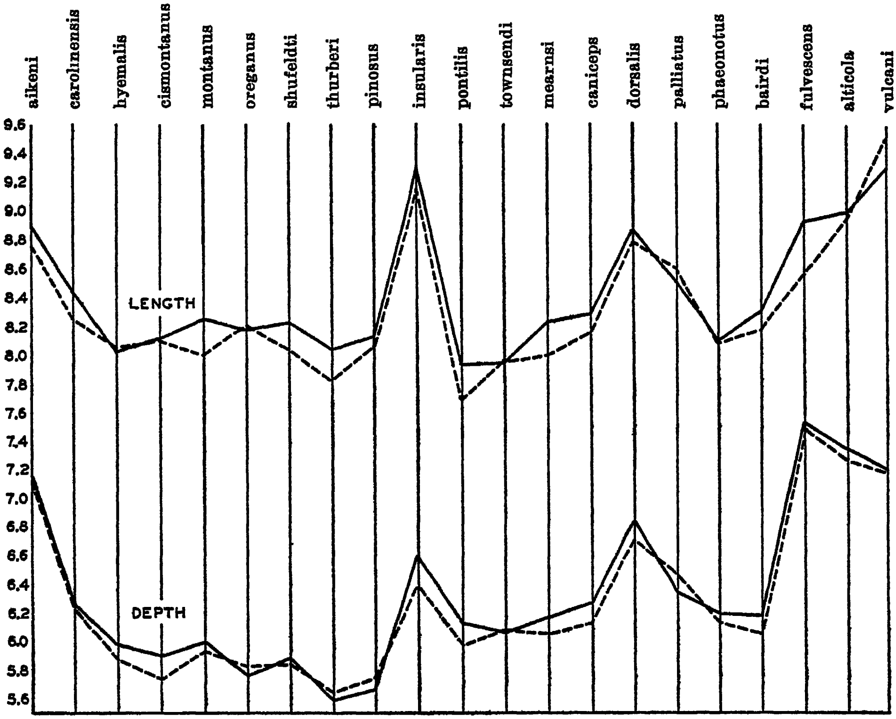

Fig. 31. Comparison of average bill length and depth, in millimeters, in juncos.

In the *oreganus* artenkreis the correlation of head and tail color is uncertain. Related races can be grouped which show correlation, but other groupings, quite as natural, reverse the correlation completely. Thus, *mearnsi, montanus, shufeldti,* and *J. o. oreganus* show a positive correlation which extends even to intraracial geographic differentiation. Also, in the *thurberi–pontilis–townsendi* group there is correlation. But the *shufeldti–thurberi* series is entirely out of keeping with this plan, as are also *pinosus* and *insularis;* it cannot be asserted that *shufeldti* and *pinosus* are unrelated to *thurberi.* They form an essentially continuous series of variant populations in which there is a negative correlation of the features in question. If the forms are grouped into primitive or light-headed (*insularis, townsendi, pontilis, pinosus,* and *mearnsi*) and advanced (*J. o. oreganus, montanus, shufeldti,* and *thurberi*) groups, the correlation within each is far from perfect.

TABLE 37

TAIL WHITE

Stages of increase in white	1 *vulcani*	2 yellow-eyed, plain-backed species	3 *caniceps* artenkreis	4 *oreganus* artenkreis	5 *hyemalis* artenkreis
1	*vulcani*				
2					
3		*alticola*			
4		*fulvescens*			
5		*J. p. phaeonotus*			
6		*palliatus, bairdi*			
7				*J. o. oreganus*	
				insularis	
8			*dorsalis*	*pinosus*	
9			*caniceps*		
10				*montanus, shufeldti*	*J. h. hyemalis, cismontanus*
11				*thurberi*	*carolinensis*
12				*mearnsi*	
				pontilis	
13				*townsendi*	
14					*aikeni*

In the *caniceps* rassenkreis, correlation of head color with tail white is negative. *Dorsalis,* however, is probably of hybrid origin, which would explain its relatively light-colored head and dark tail. Also, it is thought that the Nevada division of *caniceps* owes its slightly darker head and whiter tail to a small amount of hybridization with *J. o. thurberi.* In the yellow-eyed juncos there is a fair general correlation of head and tail color, except for *vulcani,* and except for some discrepancy when the *phaeonotus* rassenkreis and the *alticola* artenkreis are compared. In general, in this division of the genus, the differentiation of head is slight compared with that of the tail.

In those forms in which there is a eumelanin component in the back, the correlation of this with head color requires consideration. In *J. o. montanus* it was found that among individuals these areas were correlated, although in other races this was not necessarily true. To some degree they are associated interracially in *montanus* and *mearnsi,* but the back of *thurberi* has much less eumelanin than that of *oreganus*, although the two races are equally black headed. In *oreganus* the great amount of phaeomelanin masks the eumelanin or replaces it, yet the saturation of the eumelanin in the back of this black-headed race is certainly high as compared with the variants of *shufeldti* and *montanus* that have comparable extension of phaeomelanin. Among the southern Oregon juncos a general but imperfect correlation of dark pigment in back and head prevails. The chief exception to correlation occurs in *thurberi* because of its especially black head.

In the *hyemalis* artenkreis, head and back color, which are similar in tone, are closely correlated interracially. Correlation is also evident in the *alticola* artenkreis, where some dusky melanin enters into the back complex.

It follows from the foregoing discussion that eumelanin of the back and tail white also must show some correlation in certain closely related races. This is distinctly not true of *insularis* and *pinosus* in comparison with their relatives.

In groups of forms where the side coloration is grayish or has a eumelanistic component and is *confluent* with the hood area, there is interracial correlation of the color of these areas. This is manifest in the *hyemalis, caniceps,* and *phaeonotus* groups. In the Oregon juncos, the sides and head are separately controlled and the former is almost lacking in eumelanin; consequently no correlation is found. Presence and intensity of phaeomelanin in the sides are not correlated with the modifications in eumelanin. Phaeomelanins of the back and sides are not correlated.

In summary, correlated modifications in different color areas involve only the dark pigments (eumelanin), and are often imperfect even within groups of closely related races. In general, a light-colored form will to a varying degree show correlated differentiation in independently controlled parts of the plumage.

ENVIRONMENTAL CORRELATION

In matters of environmental correlation of color, the practice of treating each rassenkreis or artenkreis separately must again be followed. Intensity of pigmentation, especially of the head or hood, and the partly correlated (interracially) pattern of the tail, might by analogy with situations in other higher vertebrates (Gloger's Law) be expected to show association with rainfall and humidity. Through the northern members of the *oreganus* group this is clearly true, at least in a rough way. Just as Sumner has pointed out in *Peromyscus,* environmentally correlated characters in *Junco* by no means coincide in their occurrence with the precise geographic area over which the particular environmental conditions prevail, probably because of the effect of other factors such as barriers and population pressures. *Mearnsi, montanus, shufeldti,* and *J. o. oreganus* show the expected differences in intensity of pigment in correspondence with the environments which each encounters. In *mearnsi,* the degree of difference is unaccountably great. But southward along the Pacific coast in California the climatic gradients and racial differentiation do not correspond. Coastal *thurberi* of northern California is lighter headed than the black-headed interior bird of the more arid Sierran system. *Pinosus* of the coast is lighter headed than *thurberi.* The correlation of tail white is better than that of the head. There is no reversal of the general law, except that *pinosus* in the southern coastal district has less white than coastal *thurberi* and *shufeldti* in the more humid coastal regions to the north. In the *thurberi–pontilis–townsendi* series, correlation of head color with climate prevails, but it is surprising that a great deal of difference should exist in the birds of mountain ranges that experience relatively similar climates. The suggested archaic group of pale-headed Oregon juncos should not be forgotten in this connection. In the group comprising *thurberi, pinosus, pontilis, townsendi,* and *insularis* the correlation of tail white and climate is positive.

In the *hyemalis* artenkreis there is correlation of pale head and white tail. However, within the large range of *hyemalis,* which is extremely variable climatically, no local differentiation can be detected. If climatic correlation comes about through selection, the selection cannot be very rigid and it must be so slow that intermixture within this vast race keeps the whole at a uniform average level (see Dobzhansky, 1937, pp. 186–188).

In *Junco caniceps caniceps* the local differentiation in the Nevadan area is thought to be the result of occasional hybridization and there is, therefore, the anomalous occurrence of slightly darker-headed populations in the most arid sections of the Rocky Mountain–Great Basin area. The whiter tail of the Nevada birds might be thought of as associated with climate, yet it probably results from intermixture with *thurberi.* The summer habitat of *dorsalis,* to judge from the flora, is possibly more moist than that of *caniceps* as a whole. The head of *dorsalis* is of course lighter and the tail darker, both of which features may be attributed to the hybrid origin of the race.

In the yellow-eyed juncos both head and tail color correlate well with the degree of moisture of the habitat (see discussions under each form).

With respect to back, obviously there is environmental correlation where head and eumelanin of the back are closely associated as in the *hyemalis* group. The changes in the back in *oreganus* really comprise two phases in the seeming response to the climatic gradient of increasing moisture and humidity: (1) replacement of eumelanin by phaeomelanin, and (2) intensification of such eumelanin as persists. The back color increases from dull brown toward richer and warmer browns progressively in the following series: *mearnsi, montanus* (south), *montanus* (north), *shufeldti,* and *oreganus.* Again, there is no correlation in passing from this series to the southern *thurberi–pinosus–pontilis–townsendi–insularis* group. But within the latter there is an association with humidity. *Thurberi* and *pinosus* are ruddier than their northern counterpart, *shufeldti,* but they do have less eumelanin. Thus one phase of the correlation (eumelanin) with humidity is carried out, whereas the other is reversed at this one point. Coastal *thurberi* may owe its slightly duller coloration to extensive infiltration of *shufeldti* blood. Whatever the cause, there is a reversal of the expected trend of differentiation of coastal and interior groups in this race.

The occurrence of negative correlations in the transition from the northern to the southern group of races of Oregon juncos suggests that we are dealing with two units within each of which the association of color and climate has arisen somewhat independently. There may be some significance in the fact that the northern group is chiefly migratory, the southern more or less sedentary, although I cannot suggest a causal relation. It has seemed probable that the type of intergradation that exists between *thurberi* and *shufeldti* has not come about merely by the junction of two diverse stocks, but instead is one that results from the independent and noncoördinated change in various characters. The causative factors in the trends of differentiation in this region remain obscure. That there is no reversal of correlation in tail white and eumelanin of the back at this point should not be lost sight of.

Again it is well to stress that environmental correlation within a race is often strikingly absent. An extreme example of this is found in *pinosus:* some characters of the race appear to correspond to conditions in the humid coastal belt of central California, where the center of abundance and perhaps the center of origin of the race lie, but the scattered populations that occur in the interior arid coast ranges encounter extremes of aridity and low zonal conditions unequaled elsewhere in California in the range of any junco. Yet these birds of the interior are essentially as ruddy as the coastal populations.

Back color in the *caniceps* and yellow-eyed groups is chiefly phaeomelanin; it is of a type different from that of the Oregon juncos. It is not subject to much fluctuation, but it is slightly brighter in tone in forms that occupy especially arid regions (*bairdi* and *palliatus*).

The eumelanin of the sides, which is associated interracially with head color in all but the Oregon juncos, corresponds with climate in about the same fashion as does the head, and shows the same imperfections. The essentially phaeomelanistic sides of Oregon juncos are more ruddy in hue and are more extensive in the presumed archaic peripheral group (*mearnsi, townsendi, pontilis, insularis,* and *pinosus*). Within this group no correlation with climate is apparent. In the other Oregon juncos (*montanus, shufeldti, oreganus,* and *thurberi*), intensity, extent, and ruddiness (versus yellow) of the sides increase with increased humidity.

Among the yellow-eyed juncos, the most brilliantly colored sides occur in *bairdi* of the arid Cape district of Lower California and in *fulvescens* of the comparatively (see p. 228) arid interior of Chiapas.

In general, Gloger's Law of increased phaeomelanin and reduced eumelanin in dry hot climates finds unsatisfactory confirmation in this genus. With respect to the back area, although the eumelanin is reduced in arid regions, the phaeomelanin is also diminished; phaeomelanin is increased in some humid regions. With regard to the sides, some humid coastal races have quite as much phaeomelanin as do arid warm interior types.

The evidence for size differentiation in accordance with Bergmann's Law is unsatisfactory or wanting. In the genus as a whole, the largest species are either southern or central in location. Within the *hyemalis* group the large forms occur in the warmer southern regions. The same is true within the yellow-eyed juncos, although not perhaps within the *phaeonotus* rassenkreis (no weights for the southern member are available). Here, however, the differences in average temperature in the ranges of juncos are not known and possibly they are not great. The temperature in the habitat of the small *bairdi* should average rather high. Among Oregon juncos, the smallest forms are *pinosus, thurberi,* and possibly also *insularis* of the south; but one northern form (*montanus*) is scarcely any larger, and the largest form is *townsendi* (perhaps equaled by *mearnsi*) of Lower California.

If the principles of Bergmann's Law are valid, the low temperatures of winter with which a junco must contend may be critical factors. The small northern forms migrate from the breeding grounds and encounter no greater cold than do certain of their southern relatives. The average temperature in the wintering grounds of *hyemalis* may be less than in that of *aikeni* in the high cold plains region east of the Rocky Mountains. But still no general adherence to the Law can be discerned in the Oregon juncos. *J. o. oreganus* may be large because a large proportion of the race winters in a cool northern coastal region. But why is *townsendi* large and *thurberi* moderately small?

Relatively increased tail, foot, and bill lengths (Allen's Law) in southern members of the *hyemalis* artenkreise cannot be proved, for lack of specific data on general body size, which also increases to the south. In tail length there is, relative to wing, a definite increase; this and other changes in this ratio have already been shown to have some relation to migration (p. 357). In *oreganus,* except for wing-tail ratios, there is no consistent manifestation of Allen's Law. In *J. caniceps* and in the yellow-eyed group a definite relative increase in the foot occurs. Tail and wing appear to decrease relative to body size. Many of the races that are short winged and short tailed in comparison with their nearest relatives inhabit restricted isolated areas or veritable islands (*insularis, bairdi, fulvescens*); not all of these may be relatively short winged, as they also are small throughout—as for example, *bairdi*. Other short-winged forms are found in regions of comparatively dense forest habitat (*J. o. oreganus* and *J. o. shufeldti*) where daily flight requirements may be less (see Miller, 1931, p. 102).

DEGREE OF VARIABILITY

The accompanying graph (fig. 32) shows that variability of tail is greater than that of wing; variabilities of bill length and of bill depth are successively greater than that of tail length. The tarsus in general is similar to wing in variability, though usually slightly higher, and variabilities of middle toe and hind toe are successively, though irregularly, higher than that of tarsus (see fig. 33). Hind toe shows the highest variability of any of the mensurable characters. In general the characters with high coefficients show the most diversity in coefficients as between different races and species.

Races that are highly variable in some characters may be relatively low in others. This of course merely reflects the genetic independence of the characters. In the insular forms, *insularis, bairdi,* and *vulcani,* the coefficients are not low, even though one might suppose that these species (the first two consisting, each, of but a single population or colony) would be relatively homogeneous because of inbreeding and restocking from small residua. But certain characters are especially variable in these insular species. Probably mutation pressure is not counteracted by selection pressure to the degree that it is in other juncos. *Insularis* particularly is relatively free from predators and from competing species. It occupies ecologic situations of marked variety, and of types not ordinarily invaded by the genus.

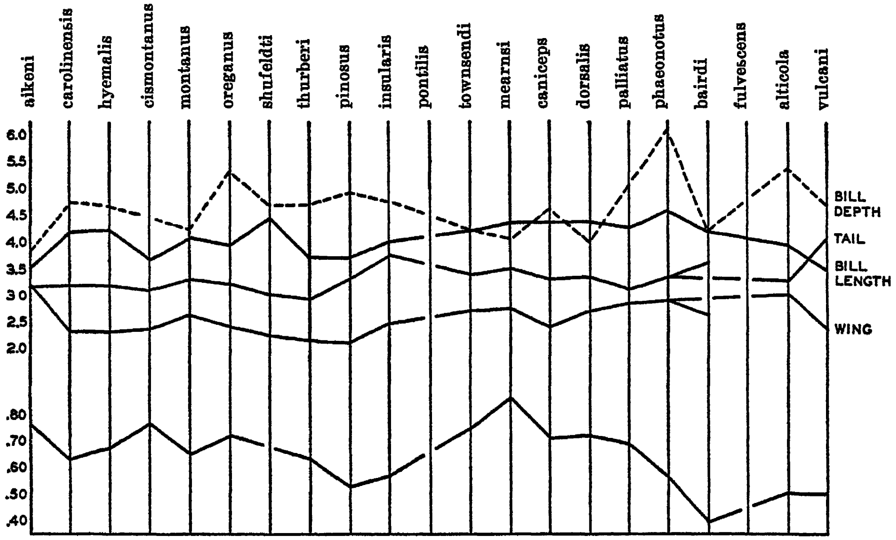

Fig. 32. Comparison of coefficients of variability of wing, tail, and bill lengths and bill depths in males of the 21 forms of the genus *Junco.* Lowest line represents coefficient of correlation of wing and tail.

With respect to measurements, certain of the races constitute mere segments of extensive geographic gradients. Values for each of these races (*montanus, thurberi, caniceps, phaeonotus*) in the graphs represent one restricted part of the race. Inclusive variability for the whole group of populations that are comprised in such a race would certainly be great. The variation in any one of the populations of the race is of "normal" magnitude. In hybrid populations it has been found that the variation usually is not greater than in the parent populations. This may be because there are involved a large number of factors, which would result in variability in generations subsequent to the F_1 that might not be noticeably higher than that of the parents. Bill and tail dimensions in certain hybrids of *caniceps* show segregation and increased variability, which suggests that a small number of factors is concerned.

Variability in coloration has not lent itself to statistical expression. Variability of measurements was not found to be uniformly high in some forms and low in others, but in coloration some are distinctly uniform throughout, whereas others are variable in almost all parts of the plumage. The northern migratory races, *J. h. hyemalis, J. o. oreganus, montanus, shufeldti,* and *thurberi,* are especially variable. However, some permanently resident forms (*phaeonotus*) in any one local province and some insular species (*vulcani*) are also distinctly variable. *Caniceps, dorsalis, palliatus, townsendi,* and *carolinensis* are relatively uniform. The most variable races with respect to color may not show high variation in any of the dimensions. Nearly all races are highly, though unequally, variable in tail pattern.

The dimensional and color characters thus far considered are all more or less quantitative in nature. They appear to provide ample material in the way of variations for further evolution of races and species. But it is clear that certain features of color are variable whereas others are not, and the variable ones have limited lines of variation which they follow.

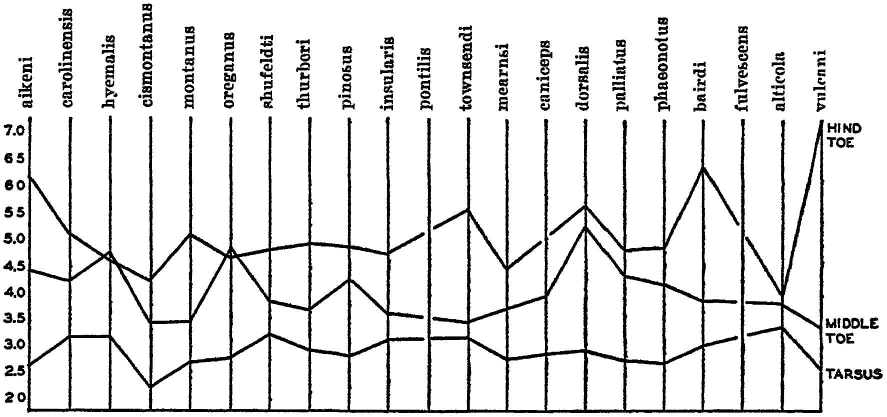

Fig. 33. Comparison of coefficients of variability of tarsal, middle toe, and hind toe lengths in male juncos.

Certain other color variations appear that resemble the larger mutations familiar in laboratory genetics. Some are like characters of other species, but others are not. They occur more frequently in some forms than in others. Because they are not merely deviations in the quantitative expression of a character, but are highly distinctive features, they serve to give an idea of the rate of occurrence and spread of new characters in a race. Probably there is no fundamental difference between this type of variant and the variants in a quantitative series. They merely are more readily detected as new departures; probably more often they depend on single factors.

The following characters are never predominant in any race: reddish brown crown feathers (not merely feather tips); phaeomelanin of areas in midventral part of hood; spotted albinism of various patterns. Others which are characteristic of some forms appear as anomalies in other races or species. These are: white wing-covert spots; reddish brown margins on wing coverts and secondaries; absence of normal reddish brown on wing; white base of culmen on an otherwise black maxilla. (Characters that almost certainly represent segregation following a more or less recent hybridization are not included.)

The percentage of occurrence of these characters is usually much too high to represent actual mutation rate. Many of the characters doubtless have been propagated through a race, following the initial mutation, so that they now are rather frequently met with. Some are probably rare recessive expressions resulting from a complex heterozygous situation that is widespread. The varying frequency of appearance may be due to factors that influence dominance in different races. The characters which are typical of certain species but which occur as anomalies in another species may be characters once common to the two, or they may have resulted from interbreeding sometime in the past. Reddish inner secondaries and white base of culmen are variants in *dorsalis,* probably of long standing, that are best explained in this way.

White wing bars occur in *hyemalis, carolinensis, caniceps, dorsalis, palliatus, mearnsi, montanus,* and *thurberi.* It is unbelievable that interbreeding with *aikeni* could have taken place to produce these variants. Also, in the races only remotely related to *aikeni* it is difficult, though not impossible, to conceive of this character as one retained from some common ancestor. The appearance of it in such diverse species and its nonlocalized occurrence in *hyemalis* favor the idea of recurrent mutation. The occurrence varies from 2.66 per cent in *hyemalis* to 0.5 in *palliatus.* The difference in occurrence in the sexes in *hyemalis* suggests that the frequency of expression is definitely modified by other factors. In *aikeni* a comparable difference obtains.

The phaeomelanistic median hood margin, which occurs more often in females than in males and which appears in 8 per cent of *mearnsi* and 25 per cent of *bairdi,* obviously is a feature that has become widely propagated in these unrelated forms following mutation. The red-crowned variant appears in *caniceps, dorsalis, palliatus, phaeonotus,* and *mearnsi.* Its occurrence varies from 6.2 per cent in *caniceps* to 0.2 in *mearnsi.* A single occurrence in the southern Mexican highlands, a region far removed from the range of *caniceps,* probably represents a separate mutation of the same kind. In *caniceps* this feature must have become considerably multiplied in the population.

The most significant aspect of these variations is the potentiality which they reveal for the formation of races or species of distinctly different plumage. The white-winged junco may be a form that has arisen from the establishment of variants of this type, although the wing bar in *aikeni* is not the most fundamental character of the species. However, the processes leading to the segregation and establishment of a character in a population, plus eventual association of characters and hence race formation, seem to be the crucial steps in speciation.

Kinds of Inheritance

Nothing can be stated with finality regarding inheritance without evidence from extensive breeding experiments. Nevertheless, a large amount of circumstantial evidence from the study of naturally occurring hybrids, correlations, and types of variability permits certain provisional statements. Even presumptions regarding heredity cannot be overlooked in considering the methods by which races and species have evolved. They may throw light on the cogency of certain hypotheses concerning origin. A summary of types of heredity will be given here without repetition of the reasons given in earlier sections for my tentative conclusions.

The most prevalent method of inheritance is apparently of the multiple-factor type. The quantitative characters of dimension, as usual, fall in this category. But there is some evidence of certain exceptions. The number of factors for any character is, as a rule, probably large. The color of the head seems to be inherited in this way, as also many of the differences in pigmentation of the back and sides.

Smaller numbers of factors, sometimes just one pair, appear to be involved (1) in presence or complete absence of eumelanin in the back, (2) in certain types of phaeomelanin of back and sides (crosses with *caniceps*), (3) in presence or absence of phaeomelanin in the sides, (4) in demarcation of the side area (crosses of *J. hyemalis* and *J. oreganus*), (5) in black base of the culmen (*dorsalis*), (6) in a certain degree of bill depth and length in *caniceps,* (7) in tail length of *dorsalis,* and (8) in the infrequent qualitative variations of plumage (see p. 367). There is nothing to indicate that characters inherited in this manner are any more fundamental than those determined by multiple factors. The characters of races in contrast to those of species cannot be distinguished by mode of inheritance or by any other means. Nevertheless, characters that depend on few factors could more readily be segregated into sharply defined species.

Dominance, sometimes variable and sex-modified, is shown by the phaeomelanin of the back of *mearnsi* over that of *caniceps;* by phaeomelanin of *caniceps* over that of *thurberi* (experimentally demonstrated; Miller, 1939, p. 212); by phaeomelanin of the sides of *mearnsi* over absence of the pigment in *caniceps;* by flesh-colored maxilla; especially the base of culmen of *caniceps* over the black maxilla of *dorsalis* (experimentally demonstrated); by bill depth of *caniceps* over that of *thurberi;* by bill length of *caniceps* over that of *dorsalis;* by tail length of *caniceps* over that of *dorsalis;* and by sides of *hyemalis* over those of *oreganus* in males.

Evidence for the interaction of sex factors (possibly through the endocrine mechanism) is found in reduction or replacement of eumelanins in females; the lesser concentration of eumelanin of the head and back in this sex; the less frequent white spots and less extensive tail spots in females; the more frequent interruption of the ventral hood margin; smaller dimensions throughout, of constant and considerable magnitude only in the wing and tail, however.

Interaction not concerned with sex has been noted between some factors for different pigments in the back and between factors for demarcation of sides and hood regions. Many of the low correlations of dimensions of parts might be thought of as resulting from interaction of factors instead of from common factors.

SEXUAL DIFFERENTIATION

The average difference in measurements of wing and tail in the sexes is fairly constant in the different juncos (see graphs). The difference usually is close to 5 per cent. The *hyemalis* and *oreganus* artenkreise are roughly similar, whereas there is slightly more sexual difference in the *caniceps* rassenkreis and slightly less in the yellow-eyed group. There is a small, almost uniform average difference in length of tarsus, which amounts to 1 or 2 per cent. Sexual difference in bill dimensions is seldom statistically reliable, but, the genus being viewed as a whole, the averages for males in the majority of cases exceed those for females. Quite as positive is the general tendency toward sexual difference in toe length.

Indices of variability and the coefficients of correlation are usually not significantly different in the sexes. No general trends are obvious in the genus.

The most obvious sexual dimorphism involves color, but this is true only of certain species. Dimorphism of the body plumage tends in the direction of reduced eumelanin and increased phaeomelanin in females. This may consist of replacement of one by the other, or extension of the phaeomelanin, or mere dilution of eumelanin (see also p. 369). In the rectrices, conversely, eumelanin is more extensive in females of all forms, except *vulcani*. The interspecific and interracial differences in dimorphism of tail pattern, unlike those of body coloration, follow no appreciable trend in the genus. Dimorphism of tail pattern is peculiarly low in *J. h. hyemalis*, whereas that of the body plumage is great. But it is not low in the related *J. h. carolinensis* and is low in unrelated forms, some of which have body plumages that are identical in males and females. It is not feasible to express color dimorphism quantitatively except with respect to intensity of head color, which displays a considerable range of sexual difference. The following list summarizes the degree of color dimorphism, chiefly of the head (for scale of numbers representing head pigmentation see p. 247):

Lacking: *vulcani, alticola, fulvescens, bairdi*
Nearly lacking: *phaeonotus, palliatus, dorsalis, insularis*
Slight: *caniceps*
Differential in head pigment (average) 1: *mearnsi, pontilis, townsendi, carolinensis*
1½: *pinosus, aikeni*
2: *montanus, cismontanus, hyemalis*
2½: *thurberi*
3: *shufeldti, oreganus*

The association of dimorphism in plumage with intense head pigmentation is frequent, but it is not consistent. The *hyemalis* group shows dimorphism equal to that in many members of the *oreganus* group, but the intensity of black or gray is generally less. No increased dimorphism appears in *J. p. phaeonotus*, nor in the dark-hooded *alticola*, compared with the lighter *J. p. palliatus*. In *thurberi* there is less sexual difference than in some related lighter-headed races; *aikeni* shows more difference than does the darker-headed *carolinensis*.

Because dimorphism of the head is associated to some degree with intensity of pigmentation, the sexual difference in color may be thought of as an interaction of certain intensity factors with sex factors (or hormones). If in the course of evolution these factors for intensification were lost, a species would revert to a less dimorphic state. Forms with dimorphism probably are not primitive, at least with regard to pigmentation, but those with low dimorphism might have secondarily attained this condition (*carolinensis?*). Reasons based on distribution already have been advanced for believing that the darkest-headed Oregon juncos are the most recently evolved forms in this artenkreis.

Retarded and female plumages often resemble fully developed plumages of duller-headed, less dimorphic forms. They do not closely resemble the rather different pattern of juvenal plumages, but they are less radically different from these than are those of adult males.

PHYLOGENY

Phylogeny within a single genus often is a matter of much uncertainty when all facts are taken into consideration. Like the problem in the crossbills (Griscom, 1937, p. 208), we do not know in *Junco* the characters of the ancestral species, and the antiquity of the characters with which we are now confronted cannot be soundly judged. Only a few speculations on the general course of phylogeny deserve attention here. Discussions of the probable origin and evolution of each form are included in the earlier parts of this paper.

The genus *Junco* seems to constitute a natural unit and, being confined to North and Middle America today, it may be assumed to have arisen in this area. Of the Emberizinae of Europe and South America, which in some measure resemble *Junco,* none has qualities which suggest that it is ancestral to the genus.

Where within the Nearctic area was the center of origin, and which juncos retain in greatest measure the ancestral condition? A few characters seem definitely to be primitive in the light of the prevalent patterns and juvenal plumages in other Emberizinae. Such are dorsal stripes, undifferentiated head region, slight sexual dimorphism, and absence or slight amount (not reduced in correlation with environment) of tail white, dark-colored maxilla, and dark iris. White wing bars are of doubtful significance in this connection. It is clear that these features, except for eye color, are more prevalent in the southern members of the genus.

Boulton (1926) has postulated, without especially convincing evidence, that the Zonotrichiae of Ridgway originated in the southern highlands of Mexico. Was this so in the genus *Junco?* The usual question is presented: Did the southern, perhaps truly primitive, juncos become crowded south along the cordillera, or did the other juncos spread out from the southern highlands as modified northward-invading forms? I fail to see grounds for a conclusive answer. The isolated southern areas may properly be viewed as an asylum for antiquated types, but are they centers of origin? Juncos as a group are adapted to Boreal conditions. It is not likely that they would have arisen on the fringes of such regions and would have come eventually to dominate them. Probably far back into the Tertiary they were adapted to Boreal situations and enjoyed a wide distribution before, or at the time, the color characters arose that now appear primitive. There must have been early geographic differentiates, some of which may have led to the basic stocks of the present rassenkreise and to isolated species; then later the races of the present rassenkreise arose as subsequent evolutionary inflorescences. Probably no form has been at a standstill with respect to evolution. The greatest environmental changes in recent geologic history have been in a broad zone bordering the glacial areas. The areas of greatest environmental stability would preserve the primitive types, and these in general must have been the southern and insular areas.

Vulcani appears to represent a primitive, possibly ancestral, stage, irrespective of point of origin. The characters common to the yellow-eyed juncos may have characterized the next stage in advance in some Tertiary species. Contemporaneously, perhaps, a more northern representative of the genus arose on the west coast that was not unlike the present *insularis* in coloration. Also there may have been *caniceps*-like and *hyemalis*-like forms in the interior and in the East. The isolation of these basic types must have been fairly complete to have permitted marked differentiation. In the glacial periods, perhaps even earlier, environmentally correlated differentiation within these Tertiary types occurred and some of them were thrown together as ranges were rejoined. *Aikeni* was established and in interglacial times it became isolated. *Caniceps* and the yellow-eyed juncos hybridized to give rise to *dorsalis*. In the Northwest a new dark-eyed group of races within the *oreganus* sphere arose which crowded out, or spread and modified, many of the ancestral paler-headed types. *Phaeonotus* and *hyemalis* proper differentiated into races, with characters that were environmentally correlated. Finally, the later glacial changes in British Columbia influenced the composition of races immediately to the south, and in the last phase of retreat permitted junction of *hyemalis* and *oreganus*, certain of whose hybrids, with favorable isolation, set up the form *cismontanus*.

INTERRELATIONSHIPS OF FORMS IN NATURE

Different forms of juncos retain a remarkable ability to interbreed, in view of the degree of structural differentiation which they display. Their readiness to accept a mate of another species is paralleled in other avian groups, yet certainly it is more pronounced than in most genera of fringillids. Little is known of the fertility of hybrids of distinct forms, but one may suppose from the successful nesting of hybrid generations in the wild that it is fairly high.

Experimental breeding in the aviary has not progressed far. A male *J. o. dorsalis* and a female *J. o. pinosus* accepted each other and mated. Three sets of eggs that were laid have been fertile, but embryos of two of the sets died shortly before hatching. The cause of death is unknown. Two normal young hatched from the third set and lived two days, when they succumbed because of dietary deficiencies (Miller, 1938*a*, pp. 92–93). In the spring of 1938, with riboflavine added to the parents' diet, two vigorous young hatched and, by providing insects, were kept alive. One young was attacked by ants when it scrambled out of the nest at eight days. The other was hand-raised from that age. In its adult plumage it served to show dominance of red back and flesh-colored bill and intermediacy (blending) of head color and size characters generally. No success was had in breeding this bird back to *pinosus* in 1939, but in 1940 a female *pinosus*, not its parent, mated and laid three sets of eggs. The first set of three hatched only one young, which seemed weak and died the same day. The other eggs had embryos that died at hatching and at about 5 days' incubation. The second set of four hatched only one young, which died at 30 hours. One of the eggs was cracked and may or may not have been fertile; the other two had embryos, one of which died at about 5 days. No riboflavine was fed to the parents in 1940 and the eggs were especially small. The eggs of the third set were somewhat larger and two of the three hatched and the young were successfully reared. The F_1 male obviously is fertile, but there may be some weakness in the cross that leads to low hatching. Again, as with the initial hybridization, the nutritional factor cannot as yet be evaluated.

Mearnsi and *aikeni* have interbred in the wild to produce at least the first generation and at least some birds that must be of later generations (see p. 351). *Caniceps* and *mearnsi* hybridize extensively when thrown together, as do *thurberi* and *caniceps* (see p. 205). A hybrid male *caniceps* × *mearnsi* has been observed behaving as though mated with a female *J. o. thurberi* (Miller, 1935, p. 468). *J. o. montanus* and *J. h. hyemalis* hybridize, but show some evidence of preference for their own kind (see p. 341).

We may conclude that a psychologic barrier to interbreeding in the wild is usually absent or is not insurmountable. Whether such an aberrant form as *vulcani* would hybridize with other juncos is doubtful. If there is no certain sterility of hybrids and if psychologic factors and differences in season of breeding in adjacent forms are of limited importance, the usual controlling factor in hybridization is geographic isolation.

Data from experimental breeding do not precisely indicate specific relationships (see Robson, 1928, pp. 14–15). Our concern is with natural processes of evolution and with the natural relations of species. Developmental failure in hybridization is but one cause of isolation; psychic, ecologic, and geographic barriers are others. Natural isolation of specific units may result from the action of several incomplete barriers of different kinds. Because the genus *Junco* somewhat resembles a group of insular forms, the members of which have the potentiality to interbreed in some measure, it might be suggested that it constitutes a single rassenkreis. Certainly the members of it are almost without exception geographically complementary. But even the most ardent exponent of the formenkreis principle would hesitate to include *vulcani* in the same *species geographicum* with the other juncos. As Rensch has stated (1934, p. 23), "systematic judgement" must be resorted to in perplexing problems where taxonomic decisions are after all purely arbitrary and involve somewhat artificially defined units.

Our problem here is to summarize in synoptic form the degrees to which the different juncos merge in nature. The series demonstrates how completely the natural relations fail to assort into a few simple categories.

a) Complete isolation at all seasons, consequently no hybridization; complete differentiation (in at least a few characters): *vulcani; alticola; fulvescens; bairdi.*

b) Complete isolation in breeding season, but junction in winter; complete differentiation: *dorsalis* and *palliatus; aikeni* and *hyemalis; aikeni* and *caniceps; mearnsi* and *hyemalis* (so far as present evidence shows).

c) Complete isolation at all seasons; some overlapping in all characters: *pontilis* and *townsendi*.

d) Complete isolation in breeding season, but junction in winter; some overlapping in all characters; no known hybridization: *pontilis* and *thurberi*.

e) Complete isolation in breeding season, but junction in winter; complete differentiation; four instances of hybridization probably arising from exchange in migration, that is, return of a bird to the breeding ground of the other species: *aikeni* and

f) Complete isolation in breeding season, but junction in winter; complete differentiation; hybrid populations in few small areas, well isolated from one or both parents: *caniceps* and *thurberi*.

g) Essentially complete isolation in breeding season, but junction in winter; complete differentiation; hybrid populations in a number of somewhat discontinuous or greatly restricted intervening breeding areas: *caniceps* and *mearnsi; caniceps* and *dorsalis*.

h) Partial isolation; complete differentiation; at least occasional (free?) hybridization in annectent areas of sparse population: *hyemalis* and *oreganus; cismontanus* and *oreganus*.

i) No physical isolation; complete differentiation; hybridization not free where both parental types are present; exchange in migration considerable: *hyemalis* and *montanus; cismontanus* and *montanus*.

j) No physical isolation; complete differentiation; free hybridization over broad area, giving appearance of "intergradation"; all characters grade and mix essentially at the same point and variability is locally increased: *mearnsi* and *montanus*.

k) No physical isolation; incomplete differentiation; intergradation chiefly through hybridization, with increased variability locally; all characters grade and mix at same point: *thurberi* and *pinosus; montanus* and *oreganus* (one phase as in *l*).

l) No physical isolation; incomplete differentiation; intergradation not the result of any immediate hybridization; some characters alter independently at different geographic points: *phaeonotus* and *palliatus; shufeldti* and *oreganus; shufeldti* and *thurberi; shufeldti* and *montanus* (southern); *montanus* and *oreganus* (one phase as in *k*); *hyemalis* and *carolinensis*.

The foregoing outline inevitably distorts the picture of the relations of any two forms. Reference should be made to the sections on relationships in the accounts of races. Particularly to be stressed is the fact that isolation is meant to indicate very considerable spatial separation. The intangible barriers (see Grinnell, 1915) that exist may not be absolute, but they are quite real, I believe, in their influence on infiltration of stocks and hence upon the type of intergradation encountered in the latter categories of the list. Particularly difficult is a brief characterization of the situation in *caniceps*, as also the relationship of the *hyemalis* and *oreganus* groups. The characterization of forms as completely or incompletely differentiated is rather arbitrary.

THE FORMATION OF SPECIES

The process of evolution is one of differentiation and segregation. The differentiation consists of separate hereditary changes, either minute or large. Evolution proceeds through the accumulation and segregation of these changes in separate populations. This study cannot touch upon the causes of mutations, nor can it produce certain types of desirable data on the selective value of characters. However, the kinds of mutations that appear and the way in which they are interrelated have in some measure been discerned. Their nature may fix the channels of future evolution, as it seems to have done in the past. The ultimate evolutionary structure is in part molded by the kinds and quantity of the building stones.

The segregating process has many phases. Some of these are demonstrable through analysis of individuals, colonies, populations, races, and species. Segregation begins with differential average occurrence of phenotypes in populations and becomes progressively more perfect through the action of a variety of isolating agencies, including genetic isolation sooner or later. Modification of populations by natural selection is a form of segregation. When full differentiation and absolute isolation are attained, further change merely increases the magnitude of differentiation; extinction of annectent groups emphasizes morphologic and physiologic separation and obscures the evolutionary pathway that has been followed. The genus *Junco* contributes a rather complete exemplification of the stages and processes that lead to the first milepost in the evolutionary path, the full species.*

In wild populations the variations in measurement, in some degree hereditary, are of roughly comparable magnitude in different forms. There is always enough latitude of variation so that some selection might take place. Racial differentiation in dimensions is rarely absolute, because with multiple-factor inheritance the restriction of variation in each race necessary for elimination of intermediates would require incredibly rigid selection.

Because wing and tail lengths are in large measure determined by common factors, their modifications can be expected to proceed in parallel more often than independently. Indeed, this is what seems to have taken place. Variations of other parts are fairly independent and permit independent differentiation. Much the same situation holds true for small differences in tone of color; but here some races and populations are much less uniform than others, permitting more modification through selection or other types of segregation. In many instances it is difficult to imagine, however, that limited variation has been brought about by more rigid selection. *Caniceps* is less variable than *J. o. thurberi* and undoubtedly it is more homozygous with respect to back color. This difference may result from some intermingling of stocks in *thurberi,* but it also may reflect a higher mutation rate, which I suspect obtains in all Oregon juncos.

Color characters of considerable magnitude which are controlled by few factors apparently spread through a population or, with comparative ease, become established in small isolated colonies. Basic mutation rate may have something to do with this, but the nature of the characters and their inheritance, especially with dominance, promote it. White wing spots, reddish brown on the crown, and other similar characters seem to arise independently from the germ line of several forms. Accordingly, it is more likely that white-winged juncos would have evolved than juncos with black spots on the breast. The paths of evolution are guided, so to speak, by the available variations, by the points of weakness (or strength) in the germ plasm where changes may take place. Much of the adherence to certain trends of modification, especially where proportion is concerned, may be necessitated by retention of functional practicability, but not so with regard to some features of color pattern. Differentiation of predominantly eumelanistic sides has occurred independently in distantly related species; this is also true of the invasion of the gray or black hood by phaeomelanin (*bairdi* and *mearnsi*). Tail white has differentiated in parallel fashion in a number of different forms that are not closely related. It may be conceded that the white has some sort of value, perhaps as a recognition mark. But the waxing or waning always follows a nearly identical series of intermediate stages. This is suggestive of the vg series of allelomorphs of *Drosophila* and their developmental interrelations as outlined by Goldschmidt (1938, pp. 229–230). Never are there predominantly transverse boundaries between dark and light areas, never a pattern with more white on a given rectrix than on its neighbor next lateral. Available variation (mutations) is of a restricted type. This means that there is a kind of orthogenesis or nomogenesis. To summarize, juncos have differentiated in characters which usually are prominent as intraracial variants, and the variants are in some measure restricted in type by the nature of the germ plasm.

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* In this discussion of speciation a fundamental similarity may be noted to many of the views expressed in Dobzhansky's (1937) excellent review of the subject, which appeared when preparation of this paper was completed. Although it has been possible to insert a few references to his work, this cannot be done for all places where our opinions coincide.

What now are the stages in segregation of variants? To begin with, colonies and populations show differences in frequency of occurrence of phenotypes (Dobzhansky, 1937, p. 63). Two phases are recognizable: (1) spotted local deviations in average occurrence, and (2) deviations as part of slight, but fairly general and often evenly graded, geographic trends. The two types may in part be coincident. The magnitude of the differences in averages ranges from the lowest limit of statistical reliability upward. Type 1, when entirely unrelated to widespread geographic trends, appears not to be correlated with local environmental differences; such segregation is found in small colonies that have some measure of isolation from neighboring populations. Examples are the weakly differentiated colony within the race *pinosus* and the Huachuca and Chiricahua populations of *palliatus*. Usually the number of characters involved is small and often there is but one character or one group of related characters (wing and tail length). It has been suggested that the fortuitous occurrence of variants within small isolated populations, or the establishment of the colony from small stocks not representative of the entire range of variability of the race, are factors in colonial differentiation. (Important and related factors are random fixation and loss of genes, Dobzhansky, *loc. cit.*, p. 131).

Differentiated colonies could subsequently spread by reason of alteration in barriers, and perhaps might supplant other juncos because of physiological or structural superiority attained in significant degree during the period of isolation. The colonial nature of the inception of such evolution would be obscured. Also, through continued isolation and further differentiation colonies might lead to such distinct forms as *aikeni*, *bairdi*, and *insularis*. The characters possessed by some of these species do show some correspondence with widespread geographic correlations. But such correlated modification of an isolated form may arise, if there is any molding force (indirect) in the environment, without there ever having been a continuous geographic gradient. In the genus there are no examples showing complete transition from the isolated colony that is not a part of a geographic gradient to a fully differentiated form. *Townsendi* and *pontilis* which might seem to exemplify this, are better explained as members of a broken-up gradient system (*pontilis* may have arisen from the junction of distinct types).

Segregation in the form of geographic gradients (type 2) can be traced from incipiency through a complete series of stages to the establishment of fully differentiated units. The causative agents in the origin of an extended geographic gradient in a character are not certainly known. The gradient results partly from the dispersal of variants (genes) from one center toward another with lowered frequency of occurrence. The extreme groups in a gradient are, so to speak, partly isolated by their own population pressures. But the gradient also results from many local intermediate frequencies established in balance with intermediate environments. Both factors are in varying measure concerned. Often gradients for two or more characters are not coincident. This suggests that diffusion started at different times and places, so that the degree of dispersal in two characters is not the same. But these characters may also be affected by different critical limits in the environmental gradient.

The stage in segregation in which there is a number of independent gradients is illustrated by conditions in *thurberi*. This form is a group of more or less continuous breeding populations through which run geographic gradients which are not all correlated and which sometimes take distinctly different directions (north to south as against east to west). The gradients differ in steepness and uniformity. Each colony or small population may have an average genetic pattern more or less peculiar to it.

How does such a complex break up into more definite units? Goldschmidt (1934) in dealing with groups of like nature in *Lymantria* found that units defined on one set of physiologic characters did not correspond to those based on another or upon structural characters. This is a good illustration of lack of correspondence in geographic or environmental trends. Nevertheless, at times we do see arising from such complexes some units the members of which have a number of characters in common that are rarely found in other units. So in *montanus*, instead of a mosaic consisting of many slightly different populations there is a polarized arrangement, with northern and southern divisions. Fifty to 60 per cent of the individuals from the two divisions can be differentiated if all characters are considered. The gradients run more or less in parallel and most of them show breaks at nearly the same point. There is a fairly marked change in average environment at this point. It would appear that the distribution of critical environments and their effectiveness as molding agents determine whether or not the mosaic will be shaped in the direction of two subraces or, as elsewhere, many variously definable subraces.

In *phaeonotus* the breaks in the parallel gradients do not coincide as well as in *montanus*, but the gradients are so extensive that the polar populations are to all purposes completely differentiated; we call the extremes races. The situation in *hyemalis* and *carolinensis* is similar, but the terminal groups are only 90 per cent differentiated. *Shufeldti* and *montanus* are about 80 per cent differentiated. The geographic differentiation in the genus tends to form race chains (Rassenketten) rather than spheres of races (Rassenkreise), because distribution is chiefly along cordilleran systems. In the horned larks (*Otocoris*), with distribution in open valleys and lake basins, the situation is reversed.

Mosaics lead to subraces and races, then, by the development of parallel gradients in different characters and by the development of coincident breaks in the gradients. The environment is basic in all this, working indirectly, we may believe. In establishing the initial gradients, slightly different rates of selection may set up different equilibria at the extremes of a geographic axis. The character of the intervening regions largely determines the gradation that results from diffusion of characters and from intermediate equilibria. If the environment changes abruptly, there is more chance that several characters will show a shift in equilibrium at this point, and there may be retardation of diffusion in one or both directions because of the change. When moreover the intermediate area is at some point less favorable to the species as a whole, a sparse breeding population results. The infiltration of characters will tend to be checked at this point, and contrasting populations will build up on either side. The few intermediates that occupy the region then become relatively more heterozygous and variable and are in fact hybrids. Of course in some instances they probably pass out of existence in certain seasons—to be replaced by individuals from either side which then hybridize. The barrier to infiltration of this type may not coincide with the point of critical environmental change that causes different equilibria. Because of population pressure and diffusion, the alterations in characters, neverthless, usually occur at the barrier. Some phases of the intergradations of *montanus* and *shufeldti,* and of *montanus* and *oreganus* (see pp. 260 and 263), constitute exceptions.

More complete isolation is exemplified by *thurberi* and *pinosus.* Areas between their ranges support small isolated breeding groups which are intermediate. This discontinuous system rather completely isolates the racial populations. Loss of such intermediate groups between *thurberi, pontilis,* and *townsendi* is the next stage in isolation. Here the only chance of interbreeding is by failure of birds to migrate in the spring (*thurberi*) and their staying to breed with members of another form. In other groups of races there is some evidence that this occasionally takes place.

The most complete isolation is that of a species such as *bairdi* in which there is no chance of mixture through stray migrants. Any further isolation must be genetic and physiologic. Prolonged geographic separation, with accumulation of adjustments to different situations, would lead to this sooner or later.

Complete isolation naturally does not bring full structural differentiation, but full differentiation cannot come about without some degree of isolation unless we assume a much more rigid selection than we have reason to think exists. Complete differentiation following isolation depends on occurrence of new characters which through selection or mutation pressure, or both, spread in the isolated population or become established by chance fixation.

The usual contributory isolation in the process of segregation is geographic. Ecologic isolation is not apparent, though ecologic differences may, as incomplete barriers, aid in determinng breaks in gradients. There is no conclusive evidence for isolation of adjacent forms through infertility. The partial isolation of *J. hyemalis* and *J. oreganus* is thought to be psychologic. This probably became manifest upon recombination of the forms after they were strongly differentiated and following complete geographic isolation.

The question may be asked, Is differentiation and segregation accomplished entirely by this essentially geographic and ecologic process? Is it possible for new variants to appear and spread through all parts of a wide-ranging species? It seems incredible that such variants could become uniformly established over a large diversified area on a more or less common time front. Inevitably, irregularities would arise, corresponding in some measure to the geographically separated units. Only through such changes as involved sterility with the parental stock could isolation be secured that would lead to a new form which occupied the same grounds as its predecessor. This is of course a method of origin for which there is evidence in various plants and animals. It does not seem to have taken place in the genus *Junco*. If it had, we might expect that two species would occupy the same range in part. Without this kind of sudden origin, the genus has progressed far in differentiation and one can hardly deny that species, even in the most conservative sense, have been formed, when we consider such types as *vulcani, alticola, bairdi,* and *insularis*.

Until segregation has proceeded to the point of adding infertility, there is always the possibility of its being broken down when forms are again thrown together in the same region. Even with infertility, unless it be quite absolute, there is some possibility. The tolerance for mates of a different type has resulted in many breakdowns in segregation in *Junco*. These have complicated the history of certain races and species. The hybridization that may result from junction of species leads to nothing completely new, but new combinations may constitute the beginning of distinct races or species, which through further change give rise to distinct phyletic lines.

What chance is there of a hybrid's becoming established over a definite area as a relatively uniform type? The possibilities would seem to lie in the possession of some advantageous quality resulting from the interaction of factors and new combinations (see Dobzhansky, 1937, p. 187), and in isolation. Isolation is the only method clearly suggested in juncos. Three instructive cases have been considered: (1) that of *caniceps* and *thurberi,* in which hybrid populations came near, so to speak, to establishing an annectent race (p.197); (2) that of *hyemalis* and *montanus,* in which certain types of hybrids became established in a somewhat isolated area that probably was rather recently made available to juncos; and (3) that of *dorsalis,* a fully established form which gives evidence in its peculiar combination of characters of origin by the hybridization of *J. c. caniceps* and *J. p. palliatus*.

Aside from the matter of origin of a race from hybrids, there is the problem of influence of occasional hybridization upon the composition of sharply defined races already extant. The problem is difficult to solve because characters added in this fashion and thoroughly mixed through a race are difficult to recognize as such. It is thought that intermixture of this kind has had an effect on *shufeldti* (see p. 261), on a subdivision of *caniceps,* and possibly on *pontilis,* if hybridization was not its actual mode of origin. Intermixture of races has contributed some of the so-called historic features of races, features that do not accord with prevailing environmental and interracial correlations.

The origin of races and species involves an interplay of many factors which, although subject to analysis, withstand resolution into a simple picture. Emphasis on a few phases of the process is certain to yield a faulty concept. It is not unlikely that in this present attempt to consider the numerous ramifications of the process as applied to a particular genus limitations will be evident to persons working with other organisms where different phases seem more apparent.

APPENDIX A

NOMENCLATURE OF RECOGNIZABLE FORMS

Junco caniceps caniceps (Woodhouse)

Struthus caniceps Woodhouse (1853, p. 202), original description
Junco caniceps, Baird (1858, p. 468)
Junco annectens Baird (1870, p. 564), part (hybrid)
[*Junco*] *cinereus* var. *caniceps,* Coues (1872, p. 141), part
[*Junco hyemalis*] var. *caniceps,* Ridgway (1873*a*, p. 613)
Junco hyemalis var. *annectens,* Ridgway (1873*b*, p. 182), part (cf. Baird)
J[*unco*]. *hyemalis annectens,* Ridgway (1874, p. 174), part
Hybrid between *oreganus* and *caniceps,* Baird, Brewer, and Ridgway (1874, p. 579), part (cf. *annectens* Baird)
[*Junco cinereus* var. *caniceps*] b. *caniceps,* Coues (1874, p. 143), part
Junco oregonus annectens, Drew (1881, p. 90), part (cf. Baird)
Junco cinereus caniceps, Drew (1881, p. 90)
Junco hiemalis annectens, Coues (1882, p. 56), part (cf. Baird)
Junco hiemalis caniceps, Coues (1882, p. 56)
Junco annecteus Morrison (1890, p. 38), part (cf. Baird)
Junco canceps Morrison (1890, p. 38)
Junco ridgwayi Mearns (1890, p. 243), part (hybrid)
Junco phaeonotus caniceps, A. O. U. Committee (1908, p. 378)
Junco oreganus mutabilis van Rossem (1931, p. 329), original description, part (hybrid)
J[*unco*]. *c*[*aniceps*]. *caniceps,* Miller (1934, p. 167)
Junco oreganus caniceps, van Rossem (1936, p. 58)

Type.—No holotype was designated by Woodhouse. With reference to the material on which the description was based, he says (p. 203): "My attention was first called to this bird by . . . Cassin, who . . . suggested an examination of several specimens of males in the collection of the Academy in connection with another in his possession, and a female in the collection made by me when attached to the Exploring party under the command of Capt. Sitgreaves, . . . in the San Francisco Mountain, New Mexico. One of these specimens in the collection of the Academy is from Mexico, the others are from Texas. My specimen is from New Mexico." These specimens may be considered to constitute cotypes. Search in the collection of the Philadelphia Academy of Sciences revealed no *Junco caniceps,* or other juncos at all readily confused with this species dating back to 1852. The only bird apparently now extant that represents the type material is No. 9281, United States National Museum. This bird evidently is the single female referred to by Woodhouse which he took on San Francisco Mountain. He speaks (1853, p. 84) as though but one junco of this new kind was taken there, and (p. 37) that at some point between Camps 15 and 18 (October 10–15, 1851; see Sitgreaves, pp. 10–12). No. 9281 bears the date, October 14, 1851. There is no reasonable doubt, therefore, that it is a cotype, and as the only known type remaining may be designated a lectotype and used as *the type.*

Type (= lectotype), no. 9281 U.S. Nat. Mus., examined by me, July, 1933.

First label, apparently original:

Fringilla oregana? Towns. | ♀ Struthus caniceps Woodhouse! | San Francisco Mt. N. M. 9281 | Oct. 14th 1851 S. W. Woodhouse MD; [reverse side] Struthus caniceps Woodhouse.

U.S. Nat. Mus. printed label, blue edged, with following data entered:

9281 | Junco caniceps (Woodh.) ♀ | San Francisco Mt. Ariz. Dr. S. W. Woodhouse; [reverse side] Oct. 14, 1851 | This is the "type" of ♀ ad | The ♂♂ mentioned in orig. descr. are in the Phila. Acad.

The skin is flattened and somewhat stained. The hood is of the gray type characteristic of the breeding birds of eastern Nevada, central and southern Utah and Colorado. It would be impossible to relate it definitely to the paler or darker variants of *caniceps* as defined in this revision (p. 182). Sides are faintly buffy (probably not merely soiling), as is frequently the condition in females of this race. Back mahogany red; secondaries edged with buff; greater secondary coverts tipped with white (for occurrence of this variation see p. 182). Bill with tip broken; base black; central region somewhat darkened, probably due to blood stain, but not black.

Type locality.—The most specific locality mentioned by Woodhouse is San Francisco Mountain, New Mexico (now Arizona). This fortunately is the place represented by the only existing type; it may be considered as the type locality, as already has generally been done. More specifically, the locality may be restricted on the basis of the known movements of the field party to their Camp 17 (October 14) on the west side of the mountain, probably Hart Spring. The locality and type of course constitute a winter or fall migration occurrence, as did also, undoubtedly, all the cotypes.

Remarks.—The description given by Woodhouse gives no good evidence of being based on more than one form; it clearly applies to the species represented by the existent type. The only doubtful point is his reference to the upper mandible as "dark brown, almost black." The frequent discoloration of the flesh-colored mandibles of *J. c. caniceps* and the presence of a discolored, injured bill in the type satisfactorily explain his statement. *J. c. dorsalis* is the only form that might be confused, and certainly its bill would ordinarily be described as black without qualification.

Junco caniceps dorsalis Henry

Junco dorsalis Henry (1858, p. 117), original description
[*Junco*] *cinereus* var. *caniceps*, Coues (1872, p. 141), part
[*Junco caniceps*] var. *dorsalis*, Henshaw (1874, p. 113)
[*Junco cinereus* var. *caniceps*] b. *caniceps*, Coues (1874, p. 143), part
Hybrid between *caniceps* and *cinereus*, Baird, Brewer, and Ridgway (1874, p. 579)
Junco cinereus var. *dorsalis*, Henshaw (1875*b*, p. 270)
Junco cinereus dorsalis, Brewster (1882, p. 195)
Junco hiemalis dorsalis, Coues (1882, p. 56)
Junco cinereous dorsalis, Morrison (1890, p. 38) (probably based on *J. c. caniceps*)
Junco phaeonotus dorsalis, Ridgway (1895, p. 391)
Hybrid between *caniceps* and *phaeonotus*, Dwight (1918, p. 299)
Junco caniceps dorsalis, Miller (1932, p. 99)

Type.—No holotype was designated by Henry. The status of the existing type, no. 9272, in the United States National Museum is not entirely satisfactory. In the museum catalogue for no. 9271 is the entry: "type, 'so stated by Baird in 1860.'" This explanation is in Richmond's handwriting. I find that there is no definite statement in the writings of Baird for this year concerning the selection of a lectotype from among Dr. Henry's material upon which the description was based. Baird does indicate that more than one specimen was used by Henry by the following statement (1858, p. 467): "The only specimens yet known of this species are those collected at Fort Thorn by Dr. Henry." What Richmond's basis was for his notation about Baird's statement of the type is not known. In Baird's reports of 1858 and 1860 the only *Junco dorsalis* listed is no. 9270. In a copy of Baird's work Richmond has changed 9270 to 9271. No. 9270 is the number of a dickcissel in the catalogue. Further information is found on the wooden block now in the main collection which refers to the type as no. 9272; on this block in Richmond's handwriting is the statement, "9271 is the type." Apparently no. 9271 was erroneously mentioned by Baird as 9270. In any event, 9271 does not now exist, so far as is known, and it may never have been formally selected as a lectotype.

No. 9272 has had the following history as written in the museum catalogue: "returned to Dr. Henry in 1859"; then later in another hand, "now in N. M." Irrespective of whether through some mix-up in cataloguing or relabeling no. 9271 became 9272, the present 9272, from the information associated with it, evidently constituted part of the material on which the description was based. It is, then, a cotype, along with the supposed no. 9271. Unless other evidence can be brought to bear concerning selection of 9271 as a lectotype, no. 9272 may be definitely selected as the type—a selection already implied by the type label which it bears. No. 9272 agrees with the original description in all matters of importance, if not in details.

Type (lectotype or cotype), no. 9272 U.S. Nat. Mus., examined by me, July, 1933. The first label, a printed Smithsonian Institution label with "type" printed on it, hence not an original label, has the following entries:

(No. 9272) Junco dorsalis. Henry | F.' Thorn. N. M. Dr. T. C. Henry; [reverse side] hardly distinguishable from J. | caniceps | except black mandible | [in pencil] throat paler as in cinereus I t

Second label, a U.S. Nat. Mus. printed red type label with the following:

9272 | Junco dorsalis | Ft. Thorn N. M. Dr. T. C. Henry: [reverse side] I.

The skin is in poor condition with neck badly twisted and feathers ruffled. The upper mandible is blackish with only a very small area slightly lighter at base of culmen (=type 8, p. 188). Bill open. Head somewhat discolored, brownish. Head and throat equal in coloration to those of birds from Mogollon Mountains, Arizona. Back dark reddish brown, hence not the bright worn red of a late summer bird. Measurements: wing, 83.3 mm.; tail, 79.5; bill length, 8.9; tarsus, 21.6; middle toe, 12.1; hind toe, 8.4. The wing measurement, which is the only one likely to afford a comparison with Henry's figures, appears not to correspond with Henry's 3.05 inches; it would be about 3.25 inches. The tail of 9272 has the following pattern; rectrix 6 pure white; outer web of fifth white, inner web 1/5 black; outer web of fourth entirely black, inner web with small white spot. Henry speaks of both 5 and 6 as white, but he might have disregarded the small amount of black on the fifth; it is not clear what was intended by his "third [from outside, = 4th] with brown on the inner edge." Measurements and tail white suggest, but do not prove, that another bird than 9272 entered into the description and may have been used more specifically in the writing of the diagnosis. The tail pattern is a common one for the race; the measurements exceed, for the most part, the averages for males, but do not represent extremes.

Type locality.—W. W. Cooke, in Bailey's Birds of New Mexico, gives the following discussion (p. 740): "The Red-backed Junco was described in 1858 by Henry, and the explicit statement is made in the original description that the type locality is Fort Thorn. This has been accepted without question as the actual type locality, but in a publication made in 1859 giving a summary of all his bird observations in New Mexico, Henry says of *Junco dorsalis* 'Found only near Fort Stanton, among the mountains, where I should judge they nested. Never observed during winter.' The species is now known to be a common breeder near Fort Stanton, while it does not breed at Fort Thorn and occurs there only in migration or in winter, at which season Henry says he has never seen it. Rereading the original description with these facts in mind it is evident that the locality Fort Thorn belongs under the preceding species, *Toxostoma dorsalis* = *Toxostoma crissalis,* which has no type locality ascribed to it, and by a printer's error was placed under *Junco dorsalis.* The real type locality of the Red-backed Junco is therefore to be considered as Fort Stanton." As further aspects of this problem I would direct attention to the fact that the original label is lacking from no. 9272 and that no date is given. From 1854 to 1858 Henry had headquarters at Fort Thorn, yet during this period he visited other localities, Fort Stanton among them, in 1855, and perhaps also at other times. Probably specimens were sent in from Fort Thorn without details concerning locality, or else in Washington an error was made in providing the label now on the specimen, which may have been made to correspond to the faulty (?) locality in the original description. Although no. 9272 is not a worn breeding bird, it could easily be an early spring bird taken on the breeding grounds. As further substantiation of the opinion that Henry found the bird on the breeding grounds, and hence not at Fort Thorn, is his statement (1859, p. 107): "This species is an excellent songster." I concur, therefore, with Cooke in considering Fort Stanton, Lincoln County, New Mexico, as the type locality.

Remarks.—With doubt remaining concerning the exact status of the type, there is, nevertheless, nothing about the description or existing type to suggest that the name *dorsalis* applies to any other than the black-billed (maxilla), pale-headed race of *Junco caniceps* for which it is currently used.

Junco phaeonotus palliatus Ridgway

[*Junco caniceps*] var. *cinereus,* Henshaw (1874, p. 113), part
Junco cinereus, Henshaw (1875*a*, p. 328), part
Junco hiemalis cinereus, Coues (1882, p. 56), part

J[*unco*]. ***cinereus palliatus*** Ridgway (1885, p. 364), original description
Junco palliatus, Sharpe (1888, p. 655)
Junco phaeonotus palliatus Ridgway (1895, p. 391)

Type.—Ridgway in the original description designated no. 68817 U.S. Nat. Mus. as the type. This bird examined by me, July, 1933. First label a printed National Museum label with the following entries:

68817 | Junco cinenus ♂ ad Sep. 19–1874 | Mt. Graham Ariz — H W. Henshaw; [reverse side] I.

Red, printed type label:

68817 | Junco cinereus palliatus Ridgw. | Mt. Graham, Arizona. H. W. Henshaw; [reverse side blank].

Skin only slightly dirty. Reddish brown extensive on secondaries and coverts. Bill black above, yellow below. Tone of grays as in resident birds of Chiricahua Mountains, with only a trace of pale smoke gray on sides. Measurements: wing, 74.0 mm.; tail, 70.4; bill length, 8.3; bill depth, 6.1; tarsus, 20.7; middle toe, 11.6; hind toe, 8.9. Tail pattern: outer web of sixth rectrix nearly pure white, inner web ¾ white; outer web of fifth rectrix black, inner web ½ white; outer web of fourth rectrix black, inner web with white spot. The tail pattern is a common one, about average for *palliatus* of Arizona; measurements except for hind toe are below average for both males and females. Those for wing and tail are so small as to suggest strongly that the bird, which was taken in September, was missexed and really was a female.

Type locality.—Mount Graham, Graham or Pinalino Mountains, Graham County, Arizona. Henshaw collected in the "pineries" (1875, p. 140). These mountains support a permanently resident population that breeds in the coniferous forests. The type almost certainly was a bird that had bred locally. Some of Henshaw's September specimens were juveniles. No migratory movements are known and the only other breeding grounds for this form north of the Graham Mountains is Pinal Mountain, which has a very small population.

Remarks.—No question attaches to the application of the name *palliatus.* Fortunately the type is from a part of the range of the race where there is none of the nomenclaturally confusing modification in the direction of *Junco phaeonotus phaeonotus.* Although *dorsalis* breeds to the northeast of the Graham Range, across the Gila Valley, there is no known hybridization to cause complications.

Junco phaeonotus phaeonotus Wagler

Fringilla cinerea, Swainson (1827, p. 435), preoccupied by *Fringilla cinerea* Gmelin 1788
J[*unco*]. *phaeonotus* Wagler (1831, p. 526), original description
[*Junco*] *cinerea,* Bonaparte (1850, p. 486)
Junco cinereus, Cabanis (1851, p. 134)
[*Junco*] *phaenotus* Bonaparte (1853, p. 918)
[*Junco hyemalis*] var. *cinereus,* Ridgway (1873*a*, p. 613)
[*Junco caniceps*] var. *cinereus,* Henshaw (1874, p. 113), part
[*Junco cinereus* var. *caniceps*] *a. cinereus,* Coues (1874, p. 143)
Junco hiemalis cinereus, Coues (1882, p. 56), part

Junco phaeonotus phaeonotus, Ridgway (1901, p. 275)
Junco phaeonotus colimae van Rossem (1938, p. 132), original description
Junco phaeonotus australis van Rossem (1938, p. 133), original description

Type.—Wagler did not specify a type, but there is a specimen in the Munich Museum (Zoologische Sammlung des Bayerischen Staats) upon which the description was based. Someone has designated it as the type and it is probably the only specimen of Keerl's that Wagler had. The description is contained in a report on the Keerl collection. Wagler may have made cursory examination of two Deppe-taken specimens, nos. 6179 and 6178, from Real Arriba and Chico, Mexico, in the Berlin Museum. The type at Munich was examined by van Rossem, August 21, 1933. He very kindly took full notes on the specimen for me and wrote on that date, giving the following particulars: "Wagler's type of *Junco phaeonotus.* No number. No sex. Wing, right 78.0 [mm.], left 77.5; tail, 69.5 [not equivalent to my tail measurements]; exp. cul., 11.1 [not equal to bill length]; tar., right, 21.6, left, broken; middle toe—claw, right, 14.1, left 14.0 [not equivalent to my measurements]. Skin taken down from mount and in bad condition. Mandible missing; maxilla blackish horn color. Plumage abraded as though collected in mid-summer—abrasion not excessive, however. Greater coverts (outer webs), 'tertials' and scapulars reddish like back, but duller. Outer tail feather white for 47 mm. along vane on outer web (terminal 17 mm., however, dusky) and for 42 mm. along vane on inner web; second lateral tail feather entirely dusky on outer web and white, terminally for 34 mm., on inner web along the vane and for 23 mm. on edge of inner web; remaining tail feathers with no white whatever. Rump inclining to olive gray.

"Three tags are attached: an old (original?) green one reading 'Junco cinereus Sw [later crossed out] Junco phaeonotus Wagler. Mexico. Keerl leg'; a new, white museum tag, 'Junco phaeonotus Wagler. Mexico. Keerl coll.'; and finally the red type tags in Hellmayr's handwriting."

Type locality.—Mexico is all that is indicated on the type and by the context of Wagler's article that contains the description. It is not known where Keerl obtained specimens, but from knowledge of the distribution of other species which he secured the locality was apparently somewhere in the southern Mexican Plateau, and certainly not anywhere near the range of *palliatus.*

Remarks.—The tail pattern of the Keerl specimen is the type that is most prevalent in populations of *J. p. phaeonotus* from the southern Mexican Plateau, although such a pattern is not unknown in *palliatus.* Measurements, where comparable, are close to the average for males of *J. p. phaeonotus.* Significant is van Rossem's description of the rump as inclining to olive gray, thus indicating the darker more olive rump of the southern race. Wagler's description clearly represents the species *phaeonotus,* but there is nothing in it that would indicate racial characters.

Junco bairdi Ridgway

Junco bairdi Ridgway (1883, p. 155), original description
Junco hiemalis bairdi, Coues (1887, p. 875)
Junco oreganus bairdi, Hellmayr (1938, p. 551)

Type.—Ridgway designated as types nos. 89811 ♂ ad. and 89810 (sex not determined) of the U.S. Nat. Mus. Subsequently someone has selected 89810 as *the type* (lectotype), even though it was mentioned after 89811 in the original description. Ridgway may have made this selection himself. Indication of this selection appears in penciled notations on the labels, apparently in Richmond's handwriting.

Type, no. 89810 U.S. Nat. Mus., examined by me, July, 1933. Skin taken down from mount, in good condition. Two labels attached. The first is a Smithsonian Institution, National Museum label with "Explorations in Lower California" printed across the top; it has the following entries:

89810 | Junco ? new species? ♂ [sex mark in different hand?; mark has been made over original; according to description, sex not determined at time of preparation] | Laguna feb 2 1883 L. Belding [name in print]; [reverse side] Junco bairdi Belding | Iris bright yellow | Type I [in blue pencil].

Red type label of U.S. Nat. Mus. with the following:

89810 | type of [printed] Junco bairdi ♂; [reverse side blank].

Cotype, no. 89811 U.S. Nat. Mus. Skin somewhat flattened. Two labels attached. First label of same kind as on type with respect to printed matter, with following entries:

89811 | } iris color of ripe oranges in | all shot about a dozen | Junco ? iris bright yellow | Laguna feb 2 1883 | under mandible bright yellow; [reverse side] Junco bairdi Belding | Type I [purple stamp] I [blue pencil].

Second label a printed type label with the following:

89811 | not the [inserted in pencil before the word type] type of [printed] Junco bairdi Belding | Laguna L. Cal. { Feb 2 1883 } L. Belding; [reverse side] not the real | type! [in pencil, I believe Richmond's handwriting] I.

The type, no. 89810, shows coloration characteristic of the species. Plumage appears slightly stained, hence pileum relatively dark, and reddish brown of back slightly darker. Pale gray of throat tinged with buff. Maxilla light horn; mandible yellow. Measurements: wing, 71.1 mm.; tail, 69.4; bill length, 8.0; bill depth, 5.8; tarsus, 19.6; middle toe, 11.3; hind toe, 6.9. Tail pattern: outer web of sixth rectrix white, inner web with trace of black; outer web of fifth rectrix white, inner web half white; outer web of fourth rectrix black, inner web with small white spot. Wing and tail measurements are above average for males, hence the sex as subsequently added to the label probably is correct. Measurements of bill and feet are distinctly below average and that for the hind toe is a minimum extreme.

Cotype, no. 89811 U.S. Nat. Mus., coloration characteristic; plumage not so much stained as in 89810, and reddish brown of back relatively light. Pileum partly overcast; and throat and breast buff edged. Measurements: wing, 67.8 mm.; tail, 66.3; bill length, 8.4; bill depth, 5.9; tarsus, 19.5; middle toe, 10.8; hind toe, 7.5 mm. Tail pattern: outer web of sixth rectrix white, inner web nearly pure white; outer web of sixth nearly pure black, inner web ⅓ white; fourth rectrix all black. No sex mark appears on the labels, although Ridgway (*loc. cit.*) listed 89811 as a male. The wing and tail measurements are inconclusive, falling between the averages for males and females.

Type locality.—Laguna [=La Laguna], Sierra de la Laguna, Cape district, Lower California, Mexico.

Junco fulvescens Nelson

Junco fulvescens Nelson (1897, p. 61), original description
Junco alticola fulvescens, Dwight (1918, p. 302)
Junco phaeonotus fulvescens, Hellmayr (1938, p. 554)

Type.—Nelson designated no. 14906 U.S. Nat. Mus., Biological Survey Collection, the type; original number, 3079. This bird examined by me, July, 1933. Original printed label headed "Biological Explorations, U.S. Dept. Agl.," with the following entries:

143906 [vertical line at left] | ♂ | San Cristobal Sept 2 1895 [year printed] Chiapas, Mexico | Nelson & Goldman; [reverse side, vertical entries] 143906 [at left] | 3079 [at right].

Red type label with printed caption as on first label with the following:

143906 [vertical] | Junco fulvescens, Nelson ♂ | San Cristobal. Sept 21, [remainder printed] 1895, Chiapas, Mexico | Nelson & Goldman; [reverse side] 143906 [diagonal] | *Junco fulvescens* | 3079 [vertical].

Type comparable to others of the original series taken by Nelson and Goldman. Skin in good condition. Measurements: wing, 74.8 mm.; tail, 69.6; bill length, 9.5; bill depth, 7.6; tarsus, 22.8; middle toe, 12.9; hind toe, 9.7. Tail pattern: outer web of sixth rectrix, ½ white, inner web ¾ white; outer web of fifth rectrix black, inner web ⅓ white; fourth rectrix all black. Measurements above average for males throughout, but extreme only with respect to bill length. Tail pattern more or less average for the series. Type was in process of molt, the back plumage still consisting of worn reddish feathers.

Type locality.—San Cristóbal, Chiapas, Mexico.

Junco alticola Salvin

Junco alticola Salvin (1863, p. 189), original description
[*Junco hyemalis*] var. *alticola,* Ridgway (1873, p. 613)
[*Junco caniceps*] var. *alticola,* Henshaw (1874, p. 113)
[*Junco cinereus*] var. *alticola,* Baird, Brewer, and Ridgway (1874, p. 580)
Junco alticola alticola, Dwight (1918, p. 302)
Junco phaeonotus alticola, Hellmayr (1938, p. 554)

Type.—Salvin designated no type. Sharp (1888, p. 657) lists the four specimens in the British Museum that were taken by Salvin prior to the publication of the description. Two of these, the birds first taken and the only ones of 1861, are designated types of the species. The first-named bird is unsexed; it is the only one now bearing a type label in the British Museum. The other bird taken in 1861, a female, is also present. The unsexed bird, no. 85.12.14.984, appears to be a legitimate type (lectotype) selected from the original series used by the describer.

Type no. 85.12.14.984 Brit. Mus. examined by me, July, 1934. Skin in good condition, though slightly flattened. Bill open. Three labels attached. The first, apparently the original:

Junco alticola | Pine Forest Volcan de Fuego | November 1861   763; [reverse side] iris 88 white [underline in pencil].

Second label:

[Left-hand section] E. Mus. [printed] | Nov. | 1861 | O. S. and F. B. G.; [right-hand section] Junco alticola Salvin | Pine forest Volcan de Fuego, Guatem. | Fig *BCA O. Salvin   763; [reverse side] 10 [on a blue paster] A [in red] | 85.12.14.984.

Third label, red:

[Vertical printing on left margin] British Museum | Type [printed] Junco alticola Salv. | Salvin, P. Z. S. 1863, p. 189 | Loc. Pine forest Volcan de Fuego, Guat; [reverse side] Brit Mus. Reg [printed] | 1885.12.14.984 | collected by O. Salvin in Nov. 1861 | Salvin-Godman Collection.

Type comparable in coloration to series in British Museum; lower mandible black basally, unlike normal *alticola*, tip yellowish; maxilla black. Measurements: wing, left, 78.1 mm., right, 78.5; tail, 74.7; bill length, 9.3; tarsus, 23.5; middle toe, 13.5; hind toe, 10.4. Tail: outer web of sixth rectrix nearly pure black, inner web $\frac{2}{3}$ white distally; outer web of fifth all black, inner web $\frac{1}{5}$ white distally; outer web of fourth all black, inner web with minute white tip. Measurements for wing and tail are well above average for males; they are above the limits of the standard deviation, but are not extreme. The bird is, therefore, almost certainly a male. Bill and hind toe are distinctly above average; tarsus and middle toe are near average for males. The tail pattern is made up of feather types that are well represented in the population.

Type locality.—Pine Forest, Volcán de Fuego, Department of Sacatepéquez, Guatemala. Salvin indicates that the species occurs at 8000 feet, but this does not necessarily mean that the type was taken higher on Volcán de Fuego; in the light of the statements made by Salvin and Godman (1886, p. 374), it probably was taken between 10,000 and 12,000 feet.

Junco vulcani (Boucard)

Zonotrichia vulcani **Boucard (1878, pl. 4, p. 57), original description**
Junco vulcani**, Ridgway (1878, p. 255)**

Type.—Boucard designated no type; he mentions (p. 57) "Several specimens from the Volcano of Irazu, obtained at the altitude of 10,000 feet." I am greatly obliged to Mr. A. J. van Rossem for examining the two Boucard birds, male and female, which are marked as types in the Paris Museum. The birds would appear to be valid types since they have been selected by someone from the author's original material. They should be regarded as cotypes. It might be appropriate at this time to designate the male as *the type,* a lectotype, as there is no indication of previous selection of one in preference to the other. Van Rossem, at the Paris Museum on July 25, 1933, made the following notations: "Two birds in the Boucard Collection. . . . Unmounted skins in fair condition though in somewhat abraded plumage. Each still bears the original field tag in (I presume) Boucard's writing | 'Volcan d' Irazu 5/77' | one is marked '♂'—the other '♀'. On the face of the labels is written, just above the locality, | Zonotrichia volcani | type | . Later tags with the well known Boucard Museum label read: Museum [vertical at left] | Zonotrichia vulcani ♂ | Col. [printed] Boucard Volcan Irazu | Costa Rica | 1877 | Type of species ♂ [In English as written] | Boucard [vertical at right]. The new tag on the second specimen is identical with the first save that it bears the ♀ sex mark."

Type locality.—Volcán de Irazú, 10,000 feet, Costa Rica.

Remarks.—Van Rossem makes no comment on the characters of the types. The birds are obviously the same as those subsequently taken from Volcán de Irazú and called *vulcani*. The original description, and especially the figure, fully identify the name with series which have been examined.

Junco oreganus mearnsi Ridgway

Junco annectens Baird (1870, p. 564), original description; part (hybrid *mearnsi* × *caniceps*); all of some authors
Junco oregonus, Merriam (1873, p. 681), part
Junco hyemalis var. *annectens*, Ridgway (1873*b*, p. 182), part (cf. Baird)
[*Junco oregonus*] var. *annectens*, Henshaw (1874, p. 113)
J[*unco*]. *hyemalis annectens*, Ridgway (1874, p. 174), part
Hybrid between *oregonus* and *caniceps*, Baird, Brewer, and Ridgway (1874, p. 579), part (cf. *annectens* Baird)
[*Junco cinereus* var. *caniceps*] b. *caniceps*, Coues (1874, p. 143), part
Junco oregonus annectens, Drew (1881, p. 90), part (cf. Baird)
Junco hiemalis annectens, Coues (1882, p. 56), part
Junco ridgwayi Mearns (1890, p. 243), original description; part (hybrid)
Junco mearnsi Ridgway (1897, p. 94), original description
Junco montanus, Macoun (1904, p. 505), part
Junco hyemalis mearnsi, American Ornithologists' Union Committee (1908, p. 378)
Junco mearnsi mearnsi, Dwight (1918, p. 296)
Junco insularis mearnsi, Dwight (1919, p. 287)
Junco (oreganus ?) mearnsi, Hellmayr (1938, p. 551)

Type.—Ridgway designated no. 11164 U.S. Nat. Mus. as the type. This bird examined by me, July, 1933. Skin taken down from mount. Three labels. Original, a printed Smithsonian Institution–South Pass Wagon Road Exp. label with the following entries (parts in italics printed):

No. 11164 Junco oreganus ♂ 177 | *Fort Bridger Utah,* (*Camp Scott*) apr. 12, *1858*. C. Drexler.

Second, a printed Smithsonian Institution–National Museum label with the following:

11164 | Junco oreganus | Ft. Bridger, Utah Drexler; [on reverse side] April 12, 1858.

Third, a Smithsonian Institution–National Museum type label bearing the following:

Type of Junco mearnsi, Ridgway.

Type specimen characteristic of the species. Depth of head color of type 10 (see p. 245). Back of ruddier type, 2*c* (see p. 247); there is none of the distinctly reddish brown color of *caniceps*, of certain *mearnsi* × *caniceps* hybrids, and of the types of *annectens* and *ridgwayi*. Measurements: wing, 82.6 mm.;

tail, 77.4; bill length, 7.9; tarsus, 21.1; middle toe, 11.7; measurements of feet possibly affected by former mounting of skin. Tail pattern: rectrices five and six pure white; outer web of fourth rectrix nearly pure black, inner web ⅓ white. Wing and tail slightly above average for males; bill distinctly below average; foot parts large, but measurements probably not to be relied upon. Tail pattern of most prevalent type in all respects.

Type locality.—Camp Scott, Fort Bridger, Uintah County, Wyoming. This locality is one at which juncos may breed. The breeding population consists, however, of *caniceps* or *caniceps* × *mearnsi* hybrids. There is no evidence of "pure-blooded" *mearnsi* breeding there, though this may possibly occur; it is probable that the *mearnsi* characters of hybrids were introduced by a pure *mearnsi* breeding there at some time. The type specimen, taken April 12, may well have been a migrant.

Remarks.—The name *annectens* was used extensively for this race, which now is properly called *mearnsi*. This name and *ridgwayi* are based on types that are hybrids of *mearnsi* and *caniceps*, as Ridgway (1897, p. 94 and 1901, p. 276) has shown. Both types are red backed (*caniceps*) and pink sided (*mearnsi*), hence with equal affinities to the two parental types. Therefore, they cannot arbitrarily be assigned to either of the parental forms and the names cannot be applied to a "pure" population. For details about types of *annectens* and *ridgwayi* see pages 405 and 406.

Junco oreganus montanus Ridgway

[*Struthus*] *oregona,* Bonaparte (1850, p. 475), part
Niphoea oregona, Baird (1853, p. 316), part
Struthus oregonus, Woodhouse (1853, p. 83), part
Junco oregonus, Baird (1858, p. 466), part
[*Junco hyemalis*] var. *oregonus,* Ridgway (1873*a*, p. 613), part
Junco hyemalis oregonus, Ridgway (1875, p. 19), part
[*Junco hyemalis*] c. *oregonus,* Trippe (1874, p. 145), part
Junco hiemalis oregonus, Coues (1882, p. 56), part
Junco hyemalis shufeldti Coale (1887, p. 330), original description, part
Junco shufeldti, Sharpe (1888, p. 840), part (cf. Coale)
Junco oregonus shufeldti, Mearns (1890, p. 244), part
Junco hiemalis shufeldtii Rhoads (1893, p. 63)
J[*unco*]. *h*[*yemalis*]. *connectens* Coues (1897, p. 94), part
Junco montanus Ridgway (1898, p. 321), original description
Junco oreganus shufeldti, Ridgway (1898, p. 321), part
Junco hyemalis montanus, American Ornithologists' Union Committee (1908, p. 378)
J. shufeldti × *J. mearnsi,* Sclater (1912, p. 381)
Junco oregonus couesi Dwight (1918, p. 291), original description, part
[*Junco*] "*transmontanus*" Dwight (1918, p. 295), original description, part (hybrid)
Hybrid between *mearnsi* and *oregonus,* Dwight (1918, p. 297)
Junco oreganus montanus, Oberholser (1918, p. 211)
J[*unco*]. *o*[*reganus*]. *couesi,* Stone (1918, p. 488), part

Type.—No. 133253 U.S. Nat. Mus. was selected by Ridgway as the type; examined by me, July, 1933. Three labels are attached. The first has the following:

Junco hyemalis | May 7, '94 Columbia Falls, Mont. RSW; [reverse side] 133253.

Second, a Smithsonian Institution–National Museum label:

133253 | Junco [cancelled: hyemalis shufeldti; interlineated:] montanus Coale | ♂ ad | Columbia Falls, Montana. R. S. Williams.

Third, a red label of the National Museum:

133253 | Junco montanus, Ridgw.; [reverse side blank].

Type specimen fairly characteristic of the southern division of the race. Head of type 7, paler than average for males (6) and palest variant normally occurring in the race; type 7 occurs in moderate numbers in all populations of southern *montanus* and occasionally in northern division. Pileum faintly streaked with different tones of black. Back, type 1*c*; thus the back is light (eumelanin), of a type frequent in southern *montanus;* at the same time it is fairly ruddy (phaeomelanin) to a degree rare in southern *montanus* but frequent in northern *montanus* of British Columbia. Sides of type 2, that is, characteristic of the race, and not suffused with eumelanin as in some; not extensively cinnamon or yellowish as in rare type 3 that resembles *mearnsi.* Measurements: wing, 76.4 mm.; tail, 69.3; bill length, 8.1; bill depth, 5.6; tarsus, 20.3; middle toe, 11.5; hind toe, 7.7. Tail pattern: sixth rectrix all white; outer web of fifth rectrix nearly pure white, inner web ⅔ white; outer web of fourth rectrix ¾ white, inner web with large white spot. Wing, and to less degree tail, distinctly shorter than average of southern division; bill less than average; feet, except middle toe, above average. Fifth rectrix blacker than average, outer vane of fourth rectrix whiter than average; but tail pattern falls within the limits of variability.

Type locality.—Columbia Falls, Flathead County, Montana. Juncos like the type breed in the vicinity of Columbia Falls. The date of collection of the type does not give assurance that the bird was breeding there, although the probability is strong that it was.

Remarks.—On page 250 will be found a discussion of the population of *montanus* from which the type was selected. The birds from the northwestern section of Montana are no more variable and no more like *mearnsi* than any of the populations from eastern Oregon, eastern Washington, or western Idaho. The type series, therefore, fits perfectly into the race, even though representing the southern division. The type itself is unfortunately a pale-headed, but not rare, extreme. Confusion in the allocation of the name *montanus* has resulted from the fact that the type series consists almost entirely of females, which naturally are pale headed, and from a general failure to appreciate the degree of paleness of the head in the females that breed throughout the interior section of the northwest. Furthermore, Ridgway selected the pale-headed variants from northwestern Montana for naming and allocated certain dark-headed breeding birds from the same localities to what was then called *shufeldti,* that is, the darker-headed groups of interior British Columbia. It is possible that Ridgway at one time thought that two species (*montanus* was described as a full species) bred side by side in this region.

In the account of *montanus* (pp. 251–257) the great range of variation of the race is stressed, as also the impracticability of subdividing it into two races. Three older names have been applied to *montanus: oreganus, shufeldti,* and *connectens.* All these are now restricted to other forms, either as usable names or as synonyms (see pp. 396, 394, and 407). *Shufeldti,* a name which recently has been used for *montanus,* is properly applied to the bird of coastal Washington and Oregon. The type is more ruddy on the back than is any interior breeding junco. Dwight (1918, p. 291) is to be credited with ascertaining this fact. What he failed to see was that the type represents at least one phase of the short-winged coastal form of Oregon and Washington. Dwight named the present *montanus* as *couesi* in the belief that Ridgway's *montanus* was a hybrid, or that at least it did not fall within the limits of his *couesi.* The name *connectens* cannot apply to *montanus,* as Ridgway has stated (1901, p. 276). The type is a female *hyemalis* in retarded plumage. Swarth's efforts to prove it was not were hampered by his inability personally to examine the type.

Junco oreganus shufeldti Coale

Fringilla oregona Audubon (1839, p. 68), part
Niphaea oregona Audubon (1839, p. 107), part
Niphoea oregona, Baird (1853, p. 316), part
Struthus oregonus, Woodhouse (1853, p. 83), part
Junco oregonus, Baird (1858, p. 466), part
[*Junco hyemalis*] var. *oregonus,* Ridgway (1873*a*, p. 613), part
Junco hiemalis oregonus, Coues (1882, p. 56), part
Junco hyemalis oregonus, American Ornithologists' Union Committee (1886, p. 275), part
Junco hyemalis shufeldti Coale (1887, p. 330), original description, part
Junco shufeldti, Sharpe (1888, p. 840), part (cf. Coale)
Junco oreganus shufeldti, Ridgway (1898, p. 321), part
Junco oregonus shufeldti, Kaeding (1909, p. 23), part
Junco hyemalis connectens, American Ornithologists' Union Committee (1910, p. 266), part
Junco oregonus couesi Dwight (1918, p. 291), original description, part
Junco oreganus couesi, Stone (1918, p. 488), part

Type.—Coale selected no. 106035 U.S. Nat. Mus. as the type; examined by me, July, 1933. Two labels are attached. The first is a printed Smithsonian Institution–Shufeldt Donation label; the words "Shufeldt Donation" have been stricken out; the label bears the following:

13 Oct. 85 | 106035 | Junco oreganus shufeldti [last name in different handwriting] ♂ | Ft. Wingate Dr. R. W. Shufeldt, U.S.A. | N. Mexico; [on reverse side] W 78 3.15×2.72 | 106035.

Second, a U.S. National Museum–Smithsonian Institution label:

[Cancelled: 106033] | 106035 | type of [printed] Junco hyemalis shufeldti | Coale; [reverse side blank].

Type specimen a relatively ruddy-backed Oregon junco, of class *ob* (see p. 271); the head is of about type 4 (p. 247), with some buff on the nape; sides army brown, thus with noticeable eumelanin component. Measurements: wing, 79.2 mm.; tail, 82.5; bill length, 8.2; bill depth, 5.5; tarsus, 20.2; middle toe, 11.6; hind toe, 8.2. Tail pattern: rectrices 5 and 6 all white; outer web of rectrix 4 nearly pure black, inner web with white spot.

Type locality.—Fort Wingate, McKinley County, New Mexico. This locality is, of course, remote from the breeding range of *J. oreganus. Montanus* and *mearnsi* are the most abundant races of Oregon juncos in this region in the winter.

Remarks.—The application of the name *shufeldti,* on the basis of the type, to one of the three dark-headed races of the Northwest presents a problem. Unfortunately the type has coloration of a kind found only in the coastal forms, and wing and tail length more like the average of interior birds. The intention of the describer, and certainly of Ridgway as quoted by him, was that the name should apply to the interior bird (now *montanus*) with a dull back and long wing. Most of the specimens other than the type are *montanus.* Two forms are therefore included in the description. There is no alternative but to determine which breeding population the type most closely resembles, since it is not typical of *J. o. oreganus* or of the coastal bird of Oregon and Washington, or of the interior bird of these states and British Columbia. The evidence is as follows. The type has a moderately ruddy brown back, type *o,* which has not been found in interior birds. (There is a single exception in the Hazelton breeding population which may be intergradient toward the coastal *J. o. oreganus.*) Type *o* is an intermediate type between *J. o. oreganus* and the coastal bird of Oregon and Washington, but it occurs in about 10 per cent of *J. o. oreganus* and in 10 per cent of Washington birds from the Cascade Mountains; it is the dominant type in the Vancouver Island intermediates (see p. 268). These considerations would seem to rule out the interior bird, which, therefore (see p. 392), must be called *montanus.* The wing and tail of the type, although long and equal to those of average *montanus,* do not exceed the maxima for the coastal forms; the measurements fall within the highest 5 per cent. Other measurements are not diagnostic individually so far as *montanus* is concerned, nor is the tail pattern.

There remains the problem of whether the type of *shufeldti* is *J. o. oreganus* (as Dwight thought, 1918, p. 291) or a member of the coastal Oregon-Washington race. The back is undoubtedly intermediate and is not more characteristic of one than of the other. The tail pattern is of an average type for coastal Oregon and Washington, but it is a type rare in *J. o. oreganus.* A pure white fifth rectrix, for example, occurs only in 7 per cent of *J. o. oreganus* but in 67 per cent of the other race. The type does not show excessively ruddy sides such as are found in many *J. o. oreganus.* The measurements of the feet are intermediate between the averages of the races. It may be concluded that the type is an intermediate but that the sum total of characters relates it more closely to the birds of coastal Oregon or Washington. It could conceivably have arisen either in the breeding range of *J. o. oreganus* or in that of the more southern race; the probabilities favor the latter. The best policy in nomenclature is to conserve familiar names when this is reasonably justified. The name *shufeldti* cannot be established as a synonym of *J. o. oreganus.* If the type is an intermediate, it is not closest to *J. o. oreganus.* Therefore *shufeldti* should be used for the race of western Oregon–western Washington. This usage has an advantage in that this name is currently applied to this race as well as to much of *montanus* as I have defined it.

The occurrence of a bird, such as the type of *shufeldti,* in New Mexico, far southeast of its breeding ground, is unusual. Nevertheless, some other *shufeldti,* and occasionally *J. o. oreganus,* cross east of the coastal mountains into the Great Basin and Rocky Mountain areas.

Junco oreganus oreganus (Townsend)

Fringilla oregana Townsend (1837, p. 188), original description
Struthus oreganus, Bonaparte (1838, p. 31)
Fringilla oregona Audubon (1839, p. 68), part
Niphaea oregona Audubon (1839, p. 107), part
Fringilla atrata Brandt (Icon. Ross. t. 2. 8, *fide* Bonaparte, 1850, p. 475)
Niphoea oregona, Baird (1853, p. 316), part
J[*unco*]. *oregonus,* Sclater (1857, p. 7)
Struthus oregonus, Newberry (1857, p. 88), part
Fringilla (*Zonotrichia*) *atrata,* Kittlitz (1858, p. 199)
[*Junco hyemalis*] var. *oregonus,* Ridgway (1873*a*, p. 613), part
Junco hyemalis oregonus, Ridgway (1875, p. 19), part
Junco hiemalis oregonus, Coues (1882, p. 56), part
Iunco oregonus, Hartlaub (1883, p. 272)
Junco oreganus oreganus, Ridgway (1901, p. 273)
Junco h[*yemalis*]. *oreganus,* American Ornithologists' Union Committee (1902, p. 323)
Junco oregonus oregonus, Dwight (1918, p. 291)

Type.—No type was selected by Townsend at the time of the description of the species. Two of his specimens now bear type labels, one, no. 1947 U.S. Nat. Mus., the other no. 24048 Acad. Nat. Sci. Phila. Which of these was first selected as a lectotype is not entirely certain, but the National Museum specimen has been accepted by Ridgway and Dwight as the type. As early as 1887 in the description of *shufeldti,* Ridgway, as there quoted, indicates that Townsend's original specimen was in the National Museum collection. The Philadelphia specimen bears no date, so that it is not certain that it was one of the original series used by Townsend; but undoubtedly it was collected in the course of Townsend's stay (fall of 1834 and April, 1835, to June, 1836) in the vicinity of the Columbia River. Therefore, I will continue to consider no. 1947 U.S. Nat. Mus. as the type; it apparently was the first specimen taken by Townsend. Fortunately, the Philadelphia specimen matches the type closely.

Type, no. 1947 U.S. Nat. Mus., examined by me, July, 1933. Two labels attached. The first bears the following:

Niphoca oregona Towns. | 1947 ♂ I | Columbia River J R.T. 5 Oct. 1834; [reverse side] Junco | oregonus | Type | of species | I [on a blue paster].

Second, a printed National Museum–Smithsonian Institution type label:

1947 | Type of [printed] Fringilla oregona Towns ♂ | Columbia River — Oct. 5–1834. J K Townsend; [reverse side] 2.98 × 250 | I.

Coloration characteristic of the most completely differentiated populations of the race. Back rich bright red-brown, type *ooob,* and head dark black, about type 3. There is some buff on the nape, as is usual in fall plumage. The sides are of average intensity. Measurements: wing, 75.0 mm.; tail, 66.8; bill, 8.1; bill depth, 5.9; tarsus, 20.3; middle toe, 13.3; hind toe, 8.6. Tail pattern: sixth rectrix pure white; outer web of fifth ½ white, inner web ⅕ white; fourth rectrix (?) black. Wing and tail length and bill length average for males; bill depth slightly greater than average; tarsus somewhat below average; toes, especially middle toe, approaching maximum, hence representing an extreme of this large-footed race. Tail pattern close to the average type throughout.

No. 24048 Phila. Acad. Sci. examined by me, July, 1933. Only the red type label is attached. Skin in good condition, taken down from a mount. Label with "Academy Nat. Sciences Philadelphia" printed on it and with the following entries:

24048 | Type [printed] of Fringilla oregana Towns. | Jour. A. N. S. Phila. VII p. 188; [reverse side] "Columbia R. | "JK.T"

Coloration essentially identical with *the type;* back color *ooob*. Fairly certainly a male on the basis of the head color and wing length. Measurements: wing, 75.2 mm.; tail, 68.6; bill length, 7.7; bill depth, 5.8; tarsus, 20.9; middle toe, 11.7; hind toe, 9.3. Tail pattern: sixth rectrix pure white; outer web of fifth ⅘ white, inner web all white; fourth rectrix all black.

Type locality.—Forests near the Columbia River, more specifically the vicinity of Fort Vancouver, Vancouver, Clark County, Washington.

During October, 1834, Townsend apparently made his headquarters at Fort Vancouver, having arrived only a few days before from the interior. He moved twenty miles down the Columbia River on the first of November. The two juncos the labels of which bear dates were taken on October 5 and 16.

Remarks.—*J. o. oreganus* winters commonly in coastal Washington and Oregon. The type and other Townsend-taken specimens are all identifiable with the breeding race of southeastern Alaska and parts of coastal British Columbia; they are clearly birds that have migrated south into the breeding range of *shufeldti*. Townsend (1839, p. 346) states: "Common on the Columbia river in winter."

Junco oreganus thurberi Anthony

Struthus oregona, Heermann (1853, p. 265)
Niphoea oregona, Baird (1853, p. 316), part
Struthus oregonus, Newberry (1857, p. 88), part
Junco oregonus, Baird (1858, p. 466), part
[*Junco hyemalis*] var. *oregonus,* Ridgway (1873*a*, p. 613), part
Junco hyemalis oregonus, Ridgway (1874, p. 173)
Junco hiemalis oregonus, Coues (1882, p. 56), part
Junco hyemalis thurberi Anthony (1890, p. 238), original description
Junco thurberi, Swarth (1900, p. 39)
Junco oreganus thurberi, Ridgway (1901, p. 273)
Junco oregonus thurberi, Stone (1904, p. 583)
Junco oreganus mutabilis van Rossem (1931, p. 329), original description, part (hybrid)

Type.—A. W. Anthony designated no. 3072 of his collection as the type. This is now no. 14814 of the Carnegie Museum, Pittsburgh. Examined by me there in June, 1933. Skin in good condition, although the neck is bent. Two labels attached. First with the following (printed words in italics):

3072 | *Collection of* A. W. Anthony; *Junco oreganus thurberi* | Junco hyemalis thurberi ♂ ad | *Collector* E. C. Thurber 5-24-90; [reverse side] Wilsons Peak, Calif. | Type 14814.

Second a blue Carnegie Museum label:

14814 [vertically] *Carnegie Museum, Pittsburgh, Pennsylvania* | Type: Junco hyemalis thurberi | Anthony: Zoe, I, 1890, 238; [reverse side] = Junco oreganus thurberi | W.E.C.T.

The type is an average example of the race with respect to coloration. The back is of the common *td* type (p. 284) and the head of type 3. The sides are a light vinaceous buff. Measurements: wing, 73.0 mm.; tail, 66.2; bill length, 7.5; bill depth, 6.0; tarsus, 20.7; middle toe, 12.2; hind toe, 8.4. Tail pattern: fifth and sixth rectrices pure white; outer web of fourth rectrix ¾ white, inner web ½ white. Wing and tail are extremely short, being about equal to the minimum for males. Bill length is well below average, even for the southern populations of *thurberi;* bill depth is somewhat above average. Tarsus is especially long, but the middle toe is near average. Thus in dimensions the type is a poor representative of the race. The tail pattern is normal.

Type locality.—Wilson's Peak (= Mount Wilson), about 5500 feet altitude, San Gabriel Mountains, Los Angeles County, California.

Remarks.—The type is a bird taken on the breeding grounds. No question attaches to the application of the name to the breeding populations of interior California, of which the type, at least with respect to coloration, is characteristic.

Junco oreganus pinosus Loomis

Fringilla hudsonia, Lichtenstein (1839, p. 432), probably referred to this race, principally or entirely
Fringilla hyemalis, Vigors (1839, p. 20), probably referred to this race in part
S[truthus]. oregonus, Gambel (1847, p. 49), part
Junco oregonus, Cooper (1870, p. 199), part
Junco hiemalis oregonus, Coues (1882, p. 56), part
Junco hyemalis oregonus, American Ornithologists' Union Committee (1886, p. 275), part
Junco pinosus Loomis (1893, p. 47), original description
Junco hyemalis pinosus, American Ornithologists' Union Committee (1894, p. 47)
Junco oreganus pinosus, Ridgway (1901, p. 273)
Junco hyemalis thurberi, Fisher (1904, p. 108), part
Junco oreganus thurberi, Squires (1916, p. 202), part
Junco oregonus pinosus, Dwight (1918, p. 291)

Types.—Loomis refers to nos. 278 and 281 of the Leland Stanford Junior University Museum as types. The male, no. 278, is the first one designated and may be considered as *the type.* Types examined by me on March 8, 1935. Both in worn plumage. The type, no. 278, bears two labels. First, a Stanford Museum label with the following (italics indicate printed matter):

Leland Stanford Junior University | Type of | *No.* 278 Junco pinosus Loomis. ♂ | *Vicinity of Monterey, Cal.,* July 4, *1892;* [reverse side] 5.8 | *Collector, Leverett M. Loomis* (935).

Second, a red label:

Leland Stanford Jr. University | *Type of* ♂ Junco pinosus Loomis.; [reverse side] *described in* "The Auk," X, p. 47. | *Figured in* "The Auk," XI, pl. vii.

Cotype, no. 281, bears two comparable labels. First:

Leland Stanford Junior University | Type of | *No.* 281. Junco pinosus Loomis ♀ | *Vicinity of Monterey, Cal.,* July 4, *1892.;* [reverse side] 5.7 | *Collector, Leverett M. Loomis* (930).

Second, type label identical with that of male except for ♀ sign.

Type, no. 278, of characteristic coloration; head about type 6; back cinnamon brown, type *pdd* (see p. 291); sides ruddy, though badly worn. Measurements: wing, 69.9 mm.; tail, 58.7; bill length, 8.1; bill depth, 5.5; tarsus, 19.9; middle toe, 11.4; hind toe, 8.0. Tail pattern: rectrices 5 and 6 pure white; outer web of rectrix 4, ½ white, inner web ¼ white. Wing and tail lengths are distinctly below average, near the minimum for males; other measurements do not depart greatly from the averages.The tail is whiter than the average, especially on rectrix 4, but the pattern is not uncommon in the race.

Cotype, no. 281, characteristically colored except for back, which represents the dull extreme of the race, type *tc;* head about type 8 and sides ruddy. Measurements: wing, 66.8 mm.; tail, 59.7; bill length, 8.0; bill depth, 5.8; tarsus, 18.7; middle toe, 10.4; hind toe, 8.0. Tail pattern: sixth rectrix pure white; outer web of fifth nearly pure black, inner web nearly pure white; outer web of fourth black, inner web with white spot. Wing, tail, tarsus, and middle-toe lengths are well below averages; the other measurements and the tail pattern are near the averages.

Type locality.—Vicinity of Monterey; more exactly, woods close to Point Pinos, near Pacific Grove (see Grinnell, 1932, p. 309), Monterey County, California. The types are, of course, breeding birds, taken at a place where the race breeds abundantly.

Junco oreganus pontilis Oberholser

Junco hyemalis oregonus, Bryant (1889, p. 301), part
Junco oreganus pontilis Oberholser (1919, p. 119), original description

Type.—Oberholser designated no. 196964, U.S. Nat. Mus., Biol. Surv. coll., as the type. Examined by me in July, 1933. Plumage worn. Type bears two labels. First, a Biological Survey label with the following (italics indicate printed matter):

196964 [vertically at left] | *Biological Survey, U. S. Dept. Agriculture* | Junco o. [*cancelled:* thurberi] pontilis | *Mexico:* El Rayo *Lower Calif. Nelson & Goldman* | June 4, 1905; [reverse side] 196964 [vertically at left] 11276 [vertically at right; original number] | Hansen Laguna Mts. | type.

Second, red Biological Survey label:

196964 [vertically at left] *Biological Survey, U. S. Dept. Agriculture* | Junco o pontilis Oberholser | *Mexico:* El Rayo *Lower Calif.* | *Nelson & Goldman* | June 4, 1905; [reverse side] Hansen Laguna Mts | 11276 [vertically at right].

Type an average specimen of the race with respect to coloration; head type 6, back about type 2*c* or 3*c*, hence duller than *thurberi* of adjacent parts of California, although some tips of feathers worn and hence light colored. Measurements: wing, 75.0 mm.; tail, 67.2 (worn); bill length, 8.0; bill depth, 6.3; tarsus, 19.0; middle toe, 10.9; hind toe, 7.7. Tail pattern: fifth and sixth rectrices all white; outer web of fourth rectrix black, inner web with white spot. Wing, tail, tarsus, and middle toe minimum for males of the race; others near average. Tail blacker than average with respect to fourth rectrix.

Type locality.—El Rayo, 4700 feet altitude, Hanson Laguna Mountains (Sierra Juárez), Lower California, Mexico. El Rayo is a ranch on the western flank of the Sierra a little south of lat. 32°, 7 miles west of Laguna Hanson (Grinnell, 1928, p. 23).

Junco oreganus townsendi Anthony

Junco townsendi Anthony (1889, p. 76), original description
Junco hiemalis townsendi, Coues (1894, p. 900)
Junco h[*yemalis*]. *townsendi* Anthony (1895, p. 183)
Junco oreganus townsendi, Oberholser (1918, p. 211)
Junco mearnsi townsendi, Dwight (1918, p. 296)
Junco insularis townsendi, Dwight (1919, p. 287)

Types.—Anthony specified two types: first, male no. 2539 of his collection (now no. 14910 of the Carnegie Museum) and second, female no. 2538 (now no. 14909, Carnegie Museum). The male, the first named, may be considered as *the type*. Both the type and the cotype examined by me at Carnegie Museum, Pittsburgh, in June, 1933; skins in good condition. The type carries two labels. The first is an Anthony collection label bearing the following (italics indicate printed matter):

Collection A. W. Anthony 2539 | *Junco townsendi* | Junco townsendi 14910 ♂ | San Pedro, L. Calif. 4/28 *1889;* [reverse side] (*Type*).

Second, a blue type label:

14910 [vertically at left] | *Carnegie Museum, Pittsburgh, Pennsylvania* | *Type:* Junco townsendi | Anthony: Proc. Calif. Acad. Sci., (2) II, 1889, 76; [reverse side blank].

Cotype, no. 14909, bears two comparable labels. First:

Collection A. W. Anthony 2538 | *Junco townsendi 14909* | Junco townsendi | San Pedro. L. Calif. 4/29 *1889;* [reverse side] type.

Second, a blue label same as that of the type except for the number 14909.

Type characteristically colored, but back extremely dull; head about type 8; back, 4*c*. Cotype comparable, with back somewhat browner than average; head about type 9. Measurements (of type): wing, 78.2 mm.; tail, 72.2; bill length, 7.8; bill depth, 6.0; tarsus, 19.7; middle toe, 11.6; hind toe, 7.8. Tail pattern: rectrices 5 and 6 pure white; outer web of fourth with trace of black, inner web ⅓ black. Measurements and pattern do not depart greatly from averages for males. Measurements of cotype: wing, 74.1; tail, 68.3; bill length, 7.8; bill depth, 5.4; tarsus, 18.8; middle toe, 11.1; hind toe, 7.7. Tail pattern: rectrices 5 and 6 pure white; outer web of fourth rectrix ½ white, inner web

⅓ white. Foot measurements and bill depth distinctly below averages for females; other measurements and tail pattern close to average.

Type locality.—"San Pedro Mountain" (San Pedro on labels), Sierra San Pedro Mártir, northern Lower California.

Remarks.—The types, although taken in April, probably were on their breeding grounds. There is no doubt that they represent the breeding population of the Sierra San Pedro Mártir.

Junco insularis Ridgway

Junco insularis Ridgway (1876, p. 188), original description
Junco mearnsi insularis, Dwight (1918, p. 296)
Junco insularis insularis, Dwight (1919, p. 287)
Junco oreganus insularis, Hellmayr (1938, p. 550)

Type.—Ridgway mentioned no type in the original description. Specimens nos. 70015–70018 and 70020–70027 in the United States National Museum were listed by him. The first of these, no. 70015, was at some time selected as *the type.* This bird examined by me in July, 1933; skin in good condition. Two labels attached. First, a printed Smithsonian Institution–National Museum label with the following written entries:

70015 | Junco 10 | Guadalupe Id ♂ | E. Palmer; [reverse side] Feb. 12, 1875 JLR | I Type [in pencil].

Second, a Smithsonian Institution–National Museum red type label:

70015 | Type of [printed] Junco insularis Ridgw ♂ | Guadalupe Isld. Dr. E. Palmer; [reverse side] I.

Type, of normal coloration. Bill dark horn color at tip, along margins and at base of maxilla. Measurements: wing, 68.4 mm.; tail, 61.8; bill length, 9.6; bill depth, 6.2; tarsus, 20.7; middle toe, 11.6; hind toe, 8.4. Tail pattern: outer web of sixth rectrix ⅔ white, inner web all white; outer web of fifth with trace of white, inner web with trace of black; outer web of fourth rectrix black, inner web ½ white. Wing, tail, and bill-depth measurements slightly below average; bill length, tarsus, and middle toe above average. Tail normal, but slightly darker than average on outer webs.

No. 70023 U.S. Nat. Mus., has " 'type of ♀' " marked on back of label in pencil.

Type locality.—Northern end of Guadalupe Island, Lower California, Mexico. In the description, the occurrence of birds on board ship at the island and on the summit of Mount Augusta, 3500 feet, is mentioned. It is not certain precisely where the type was taken.

Junco hyemalis hyemalis (Linnaeus)

[*Fringilla*] *hyemalis* Linnaeus (1758, p. 183), description based on *Passer nivalis* Catesby (1731, p. 36, pl. 36)
[*Emberiza*] *hyemalis* Linnaeus (1766, p. 308)
Fringilla hudsonias Forster (1772, p. 406)
Fringilla hudsonia Gmelin (1788, p. 926)

P[*asser*]. *nivalis* Bartram (1791, p. 291, *fide* Coues, 1875, p. 351; p. 289 of reprint of 1792, which seen)

Fringilla nivalis, Wilson (1810, pp. xii and 129, pl. 16, fig. 6), part, this name used only in contents, p. xii.

Struthus hyemalis, Bonaparte (1838, p. 31)

Niphaea hyemalis, Audubon (1839, p. 106)

Euspiza [*Niphoea*] *hyemalis,* Blyth (1849, Cat. Birds Mus. Asiat. Soc. Bengal, p. 130, *fide* Ridgway, 1901, p. 280)

Niphaea . . . hudsonia, Lichtenstein (1854, Nomencl. av. Mus. Berol., p. 43, *fide* Ridgway, 1901, p. 282

J[*unco*]. *hyemalis,* Sclater (1857, p. 7)

[*Junco hyemalis*] var. *hyemalis,* Ridgway (1873*a*, p. 613)

[*Junco hyemalis*] a. *hyemalis,* Coues (1874, p. 141)

[*Junco hyemalis*] b. *hyemalis,* Trippe (1874, p. 145)

Junco hiemalis Coues (1882, p. 55), part

J[*unco*]. *h*[*iemalis*]. *connectens* Coues (1884, p. 378), original description, part

J[*unco*]. *hyemalis connectens,* Ridgway *in* Beckham (1887, p. 122), part

Junco hyemalis hyemalis, Ridgway (1901, p. 273)

There is no type. Linnaeus based his description on Catesby's account. Linnaeus characterizes the species as follows (p. 183): "*hyemalis.* 30 F[ringilla]. nigra, ventre albo. *Passer nivalis. Catesb. car.* I. *p. 36. t. 36. Habitat in* America." Although this would appear to refer to *Junco hyemalis* as now known, Catesby's more explicit account leaves no doubt. Catesby says, p. 36: "The bill of this Bird is white: The Breast and Belly white. All the rest of the Body black; but in some places dusky, inclining to Lead-colour. In *Virginia,* and *Carolina* they appear only in Winter: and in Snow they appear most. In Summer none are seen. Whether they retire and breed in the North (which is most probable) or where they go, when they leave these Countries in the Spring, is to me unknown." As Brewster (1886*a*, p. 109) has stated, this description clearly applies to the northern race of slate-colored junco. The fact that part, and not all, of the dark parts are "inclining to Lead-colour" may be taken as eliminating *carolinensis.* Also the winter occurrence suggests the prevalent flocks of the northern form rather than *carolinensis,* which, I believe, does not commonly leave the vicinity of the mountains (see p. 329).

Type locality.—In the fourth edition of the A.O.U. Check-list (1931, p. 345) the type locality is restricted to South Carolina. Catesby mentions both Virginia and Carolina, in the order given. It is not particularly significant which region is specified, as all this section of the Atlantic coast is in the winter range of the race and there is no more chance of intermixture of other races in the winter flocks in one area than in another.

Junco hyemalis carolinensis Brewster

Fringilla nivalis, Wilson (1810, pp. xii and 129, pl. 16, fig. 6), part; this name used only in contents, p. xii

Fringilla hudsonia, Wilson (1810, p. 129, pl. 16, fig. 6), part

Fringilla hyemalis, Jardine ed. Wilson's Am. Ornith., 1832, p. 272, pl. 16, fig. 6, *fide* Ridgway, 1901, p. 280), part

Junco hyemalis, Baird, Brewer, and Ridgway (1874, p. 580), part

Junco hiemalis Coues (1882, p. 55), part

Junco hyemalis carolinensis Brewster (1886*a*, p. 108), original description
Junco carolinensis Brewster (1886*b*, p. 277)
J[*unco*]. *h*[*iemalis*]. *carolinensis,* Coues (1887, p. 874)
[*Junco hiemalis*] Subsp. *a. Junco carolinensis,* Sharpe (1888, p. 649)

Type.—Brewster designated nos. 10597 and 10567 as types. The first one mentioned, the male, no. 10597, may be considered as *the type.* It is now no. 210597, Mus. Comp. Zoöl. It and the cotype examined by me in Cambridge in July, 1933. Type bears two labels. First, a Brewster Collection label with the following (italics indicate printed matter):

Junco h. carolinensis ♂ ad. Type ♂ | North Carolina (Black Mts.) Jun 2 | 1885 | [vertically at right] *No.* | 10597; [reverse side] *Collection of William Brewster* | Type | *Collection* William Brewster.

Second, a red Museum of Comparative Zoölogy label:

No. 210597 *Museum Comparative Zoology* | Cotype | Junco hyemalis carolinensis | [cancelled: *Loc.*] Brewster *coll.;* [reverse side] Auk III. Jun. 1886. p. 108.

The type is a characteristic light slate bird, with tail with maximum amount of white. Measurements: wing, 80.5 mm.; tail, 69.5; bill length, 8.4; bill depth, 6.3; tarsus, 21.3; middle toe, 13.3; hind toe, 8.8. Measurements close to average except tail and middle toe, which are below average.

Cotype, no. 210567 Mus. Comp. Zoöl. Two labels attached comparable to those of type. First:

Junco hiemalis carolinensis type ♀ ad ♀ | North Carolina (Highlands) May 28, 1885. | [vertically at right] *No.* 10567; [reverse side] *Collection of William Brewster* | Type of ♀ | *Collection* Wm. Brewster.

Second, red label:

No. 210567 *Museum Comparative Zoology* | Junco hyemalis carolinensis | [cancelled: *Loc.*] Brewster | Cotype *coll.;* [reverse side] Auk III Jan. 1886 p. 108.

Cotype pale slate, about type 9 or 10, with sides and back washed with smoke gray. Measurements: wing, 74.9 mm.; tail, 68.5; bill length, 8.5; bill depth, 5.9; tarsus, 20.5; middle toe, 11.7; hind toe, 8.7.

Type locality.—Black Mountain, Buncombe County, North Carolina. Evidently the type was taken at a higher elevation than Black Mountain Post Office, probably to the north in the Black Mountains (see label) at 5000 feet altitude or more, certainly above 4300 feet (Brewster, 1886*a*, pp. 95 and 109). The types clearly are breeding birds. The cotype was taken at Highlands, Macon County, North Carolina.

Junco hyemalis cismontanus Dwight

This synonymy includes names applied to hybrids of *J. oreganus montanus* or of *J. oreganus oreganus* with *J. hyemalis,* as it is not possible to distinguish certain hybrids from the race *cismontanus* that breeds in interior northern British Columbia (see p. 345).

Hybrid between *hyemalis* and *oregonus,* Baird, Brewer, and Ridgway (1874, p. 579)
J[*unco*]. *h*[*iemalis*]. *connectens* Coues (1884, p. 378), original description, part

J[*unco*]. *h*[*yemalis*]. *connectens* Coues (1897, p. 94), part
Junco montanus Ridgway (1898, p. 321), original description, part
Junco hyemalis × *Junco oreganus shufeldti*, Ridgway (1901, p. 276)
Junco hyemalis, Macoun (1904, p. 499), part
Junco oreganus shufeldti, Macoun (1904, p. 504), part
Junco hyemalis shufeldti, MacFarlane (1908, p. 411), part
Junco hyemalis montanus, Osgood (1909, p. 41), part
Junco h[*yemalis*]. hyemalis, Riley (1912, p. 68), part
[*Junco*] *"cismontanus"* Dwight (1918, p. 295), original description
[*Junco*] *"transmontanus"* Dwight (1918, p. 295), original description, part
Junco hyemalis × *oregonus*, Dwight (1918, p. 295)
Junco oregonus × *hyemalis*, Dwight (1918, p. 295)

Winter-taken or migrant hybrids and members of the race *cismontanus* have had various forms of the names *oreganus, shufeldti, montanus,* or *hyemalis* mistakenly or loosely applied to them. These names have been used apparently without intention of expanding their application to hybrids or to *cismontanus*. Only when they have been used for breeding *cismontanus*, or in reference to breeding range that clearly includes areas of prevalent hybridization, have they been considered by me in compiling the above synonymy.

No type was specified by Dwight, for it was his intention to suggest a name for a certain kind of hybrid without recommending its use. The name *"cismontanus"* is valid because Dwight gave an "indication" which beyond reasonable doubt fits the race to which Swarth (1922, p. 244) endeavored to apply the name *connectens* (see p. 407). This indication is contained in the following statement (1918, p. 295): ". . . east of the Rocky Mountains we have a *hyemalis* darkened or blackened by the *oregonus* strain that, for convenience, might be called '*cismontanus*.' . . . If these names [referring also to *transmontanus*] could be restricted to definite geographical areas there would be some grounds for admitting the existence of three races." This latter condition with respect to *cismontanus* is fulfilled, as shown by Swarth, and substantiation has been offered in the present study. As pointed out earlier, *cismontanus* is a group of hybrid origin, now stabilized, which occupies a geographic area in the breeding season to the exclusion of other forms. In other regions birds of identical appearance may be produced by hybridization. Thus, although Dwight coined the name solely for hybrids, it has since been found that a stabilized group indistinguishable from the hybrids exists, and the name must be used. In similar fashion the name *connectens* could have been applied, except that a type identical with *hyemalis* was selected.

Dwight's indication describes perfectly the males of the race in question. Part of the race breeds east of the Rocky Mountains, as he states. Further, there is a series of specimens in Dwight's collection that bear his penciled identification: " 'cismontanus' D." These are comparable to breeding birds from the Atlin, Carcross, and interior Stikine districts of British Columbia and southern Yukon.

Selection of type.—Since Dwight's own series was before him at the time he coined the name *cismontanus*, it is appropriate to select a lectotype from it. Accordingly, no. 402559 Am. Mus. Nat. Hist. (12281, Dwight collection) is chosen. It bears two labels (*fide* John T. Zimmer, March 24, 1938). Original label:

Junco hyemalis | 13 Feb. 05 ♂ Sumas, B. C. | Allan Brooks col.

Dwight label:

Junco o. shufeldti ♂ | B. C. Sumas. Feb. 13, 1905 | 12281 | hyemalis × oreganus D | = cismontanus | AMNH 402559.

Because Dwight is not known to have made use of any particular breeding specimens in formulating his concept of *cismontanus*, a winter-taken *cismontanus* unfortunately must be selected.

The type was examined by me in July, 1933, at the American Museum. It was compared directly with no. 44868 Mus. Vert. Zoöl., which is a typical breeding male of the race, from Carcross, Yukon Territory, taken May 26, 1924. The type, although in less worn plumage, would have been equivalent in appearance by breeding time. The only difference is that the type has a somewhat blacker head; size was not compared. The coloration of no. 44868 is as follows: sides completely slate; hood no. 6; pileum dull black; head well contrasted with back; back *aaa* (see pp. 330–333).

Type locality.—Sumas, New Westminster District (lower Fraser Valley), British Columbia. The local breeding bird in this region is *Junco oreganus shufeldti.*

Junco aikeni Ridgway

Junco hyemalis var. *aikenii* Aiken (1872, p. 201), *nomen nudum*
[*Junco hyemalis*] var. *aikeni* Ridgway (1873*a*, pp. 613, 615), original description
J[*unco*]. *aikeni*, Baird, Brewer, and Ridgway (1874, pl. 26, fig. 6)
[*Junco hyemalis*] b. *aikeni*, Coues (1874, p. 141)
[*Junco hyemalis*] a. *aikeni*, Trippe (1874, p. 145)
Junco hyemalis aikeni, Drew (1881, p. 90)
Junco hiemalis aikeni, Coues (1882, p. 55)
Junco hyemalis danbyi Coues (1895, p. 14), original description
Junco danbyi, American Ornithologists' Union Committee (1897, p. 133)

Type.—Ridgway based his description on no. 61302 of the United States National Museum. This, although not specifically mentioned as the type, is the only specimen that can be so regarded; others were not listed in the formal description. Type examined by me in July, 1933, at the United States National Museum. Two labels are attached. First, an Aiken collection label:

Collection of C. E. Aiken, [printed] ♂ 135 Peoria St., Chicago. | 1053 Junco [*cancelled:* hyemalis] var. aikeni, Ridgw. | Collected [printed] El Paso Co., Col. T. Dec. 11. 71 — Aiken [printed]; [reverse side] Type of Ridgway's description 61302 | I.

Second, a red, printed Smithsonian Institution–National Museum label:

61302 Type of [printed] Junco aikeni 1053 ♂ | El Paso Co., Col. $\left\{\begin{matrix}\text{Dec. 11}\\ \text{1871}\end{matrix}\right\}$ C. E. Aiken.

The type is a light slate-colored bird, brownish as are females and immatures. There is white on the middle secondary coverts. Measurements: wing, 84.0 mm.; tail, 78.6; bill, 8.7; bill depth, 7.3; tarsus, 21.2; middle toe, 11.6;- hind toe, 9.4. Tail pattern: fifth and sixth rectrices white; outer web of fourth rectrix ⅔ white, inner web all white; outer web of third rectrix black, inner web ⅓ white. Wing and tail are below average for males, the former nearly as short as the average for females; the hind toe is especially long; the other measurements do not depart importantly from the averages. The tail pattern is normal, but it is closer to the average for females than it is to that for males. This and other features of the type suggest the possibility that the bird may have been missexed.

Type locality.—El Paso County, near Fountain, Colorado. More specifically, Turkey Creek, "some eighteen miles southwest from Colorado Springs" (Warren, 1936, p. 235).

Remarks.—Although the type and the original specimens are winter taken, they all clearly pertain to the species that nests in the Black Hills of South Dakota.

TYPE SPECIMENS UPON WHICH DISCARDED NAMES WERE BASED

It is well to place on record information relative to types that formed the basis for certain invalid names. For some of the early names, such as *Fringilla cinerea, atrata, nivalis,* and *hudsonias,* that were relegated to synonymy, there are no types. All types connected with the more recent names have been examined. *Transmontanus,* for which there is no type, was proposed by Dwight (1918, p. 295) for a certain phase of hybrid of *J. oreganus* and *J. hyemalis.* No stable group of birds of the kind he describes exists. Hybrids with the essential characters of *oreganus,* but with partly slate-colored backs, occur within parts of the range of *montanus* adjacent to *J. h. hyemalis* or *J. h. cismontanus.* These correspond to Dwight's *"transmontanus."* The name remains that of a hybrid, then, as Dwight intended it should be.

Junco annectens Baird

Type.—When Baird (1870, p. 564) named *annectens,* he had several specimens before him, all but one of which were *mearnsi.* Ridgway (1901, p. 276) says: " . . . it is nevertheless easy, in view of the characters most prominently mentioned in the diagnosis, to determine which should be considered as the type. For instance, the phrase 'whole interscapular region . . . light chestnut rufous,' found in the description, applies only to no. 11164." With this opinion I am in agreement, but there is an unfortunate error regarding the number, which probably was incorrectly transcribed along with the data, and should be no. 10701. In Ridgway's original description (1897, p. 94) of *mearnsi,* in which he develops a similar argument for the restriction of the name *annectens* to a particular specimen, he designates no. 10701 as Baird's type and 11164 as the type of *mearnsi.* My recent examination of the types confirms this. No. 10701 is the red-backed bird, and 11164 and others are brown backed. No. 10701 is therefore a properly selected type of *annectens.*

The type bears two labels. First, a printed Smithsonian Institution–South Pass Wagon Road Exp. label:

No. [printed] 10701 [*cancelled with blue pencil:* Hybrid—J. oregonus & caniceps; *interlineated:*] annectens ♀ | 474 | Fort Bridger, Utah, (Camp Scott) [printed] May 28, 1858.

C. Drexler [year and name printed]; [reverse side, in blue pencil:] "Hybrid" [in ink:] junco ridgway Mearns. [in blue pencil:] connectens × caniceps | R.R.

Second, red Smithsonian Institution–National Museum type label:

Type of [printed] Junco annectens Baird; [reverse blank].

The back is the full reddish brown of *caniceps,* and the sides are broadly pinkish cinnamon as in *mearnsi.* Some of the secondary coverts are tipped with reddish brown. The bird is exceptionally worn for the date, May 28. It undoubtedly was breeding, unlike the type of *mearnsi* taken earlier in the season at the same locality. Measurements: wing, 78.5 mm.; tail, 69.4; bill, 8.0; bill depth, 6.2; tarsus, 20.4; middle toe, 11.7; hind toe, 7.5. Tail pattern: sixth rectrix all white; outer web of fifth ½ white, inner web with small amount of black; outer web of fourth black, inner web with white spot.

Type locality.—Camp Scott, Fort Bridger, Uintah County, Wyoming.

Identification.—Hybrid of *J. c. caniceps* × *J. o. mearnsi* (see synonymies of these).

Junco ridgwayi Mearns

Type.—Mearns (1890, p. 243) named *ridgwayi* from a type in his collection, no. 2770, now no. 52902 Am. Mus. Nat. Hist. Examined by me in July, 1933. Three labels attached. First (italics indicate printed matter):

Collected By Edgar A. Mearns M D | *No.* 2770 ♂ ad. April 22, 1884 | *Locality,* Whipple Barracks, Arizona | caniceps × mearnsi [in pencil]; [reverse side] Junco ridgwayi Mearns | 163; 257; 80; 77. | Culmen 12; tarsus 20.5; middle toe & claw 20.

Second:

Mearns | *Collection* [vertically at ends of label] | *American Museum* 52902 *of Natural History* | April 22, 1884. ♂ ad | Junco ridgwayi | Arizona. Whipple Barracks Dr E. A. Mearns; [reverse side]; No. 2770 Mearns Coll | Type of Junco Ridgwayi, Mearns | Auk, vol. p.

Third, a red printed type label of the American Museum with no entries upon it.

The type is of the same coloration as the type of *annectens;* back pure reddish brown, sides pinkish cinnamon. Measurements: wing, 79.5 mm.; tail, 74.0; bill, 8.0; bill depth, 6.4; tarsus, 20.0; middle toe, 11.5; hind toe, 8.4. Tail pattern: sixth rectrix all white; outer web of fifth white, inner web with trace of black; outer web of fourth with trace of white, inner web ¼ white.

Type locality.—Whipple Barracks (Fort Whipple at Prescott), Yavapai County, Arizona. The locality represents a winter or migration station.

Identification.—Hybrid *J. c. caniceps* × *J. o. mearnsi.* Mearns identified the type with No. 10701, U.S. Nat. Mus., the bird that later proved to be the type of *annectens. Ridgwayi* is, therefore, a synonym for the hybrid *annectens* (see p. 405).

Junco oreganus mutabilis van Rossem

Type.—No. 31,126, collection of Donald R. Dickey at the University of California, Los Angeles. Two labels attached. First:

Dickey | Col. No. 31,126 [vertically at left] Junco oreganus mutabilis Type van Rossem ♂ im | Charleston Mts., Clark Co., Nevada | Col. by A J. van Rossem | Sept. 14, 1930; [reverse

side] col. no. 31,126 [vertically at left] Collection of Donald R. Dickey ♂ im | alt. 8200 ft. Assoc. Yellow Pine | Lee Cañon AJvR. #13,221.

Second, a red type label:

Collection of Donald R. Dickey No. 31,126 | Type of Junco oreganus mutabilis van Rossem | Described in Trans. San Diego Soc. Nat. Hist., 6, no. 22, June 5, 1931, p 329.

Back of pure *caniceps* type, sharply limited. Hood not strongly set off from sides, which are gray anteriorly. Sides posteriorly partly buff, with phaeomelanin. Head as in lighter types of female *thurberi*. Measurements: wing, 78.4 mm.; tail, 70.9; bill length, 8.3; bill depth, 6.2; tarsus, 20.4; middle toe, 12.0; hind toe, 8.8. Tail pattern: sixth rectrix all white; outer web of fifth white, inner web ¾ white; outer web of fourth black, inner web with white spot.

Type locality.—Lee Cañon, yellow pine association, 8200 feet, Charleston Mountains, Clark County, Nevada. The bird, although taken in September, undoubtedly was on the breeding grounds where it was raised.

Identification.—Hybrid *J. c. caniceps* × *J. o. thurberi*. The hybrid nature of the population breeding on the Charleston Mountains has been fully discussed (see p. 189 ff.). The type is a fair representative of this heterogeneous population; it combines characters of the parent forms. The population is highly varied and there are many birds that are distinctly different from the type.

Junco hiemalis connectens Coues

Type.—Coues (1897, p. 94) states that types were selected from the Brewster Collection when he characterized *connectens* (Coues, 1884, p. 378). Allen and Brewster (1883, p. 189) mention two specimens taken by Brewster in 1882 shortly before Coues named *connectens*. The first of these two similar specimens, no. 7046, apparently was chosen as *the type*. Certainly it was one of those used by Coues, and it probably was selected by him.

Type, no. 207046 Mus. Comp. Zoöl., examined by me in July, 1933. Two labels attached. First (italics indicate print):

Collection of William Brewster | Junco h. connectens Type ♀ | Colorado (Colo. Springs) Apr. 26, 1882 *W. B.* | No. 7046 [vertically at right]; [reverse side] ♀ Type of Junco | connectens | Coues.

Second:

No. 207046 Museum of Comparative Zoology | Type | Junco h. connectens Coues | [*Cancelled:* Loc] (=Junco h. hyemalis (Linn).); [reverse side] Key N. Am. Birds 2nd Ed | 1884. p. 378.

The type was identified by Ridgway and by Dwight as an immature female *J. h. hyemalis*. Coues' description also might in part refer to such an individual of this race. Swarth (1922, pp. 244–245) in resurrecting the name for application to the Cassiar breeding bird was unable to examine the type personally. He sent some sample specimens east to Outram Bangs for comparison with the type. Bangs reported to Swarth that the type was the counterpart of no. 39957 Mus. Vert. Zoöl. from Telegraph Creek, British Columbia, May

29, 1919: " 'Indeed you would have difficulty in telling the two apart, except that the type . . . is . . . in a little more worn plumage. I can't find spring females from the east just like these, but on the other hand, autumnal females much resembling them . . . are common in our series' " (Swarth, 1922, p. 245).

It was with much interest that I compared this same no. 39957 with the type at the Museum of Comparative Zoölogy. In color values and detailed distribution of buff overcasting the similarity is very great. The overcasting on the breast of the type is a little more extensive and, as a result, the hood line less distinct. The less worn feather tips of no. 39957 conceal a slightly deeper black than exists in the type. The most important character of the type is, however, the extension of the hood mark onto the sides beneath the feather tips. Consequently the hood line is concave, not convex as in no. 39957. This was overlooked by Bangs, probably because of concentration upon the superficial buff color, but it is the crucial point in the determination. The type is, then, a fairly typical female *hyemalis* which can be matched by eastern birds. The buff overcast is a little less uniform on the breast than in the majority of female *hyemalis.*

Measurements: wing, 75.0 mm.; tail, 63.2; bill, 7.9; bill depth, 5.5; tarsus, 19.8; middle toe, 11.7; hind toe, 8.4. Tail pattern: fifth and sixth rectrices pure white; outer web of fourth rectrix nearly pure white, inner web ⅔ white; outer web of third rectrix black; inner web with small white spot.

Type locality.—Colorado Springs, El Paso County, Colorado. The locality is of course a winter or migration station.

Identification.—*Junco hyemalis hyemalis.*

Junco oregonus couesi Dwight

Type.—No. 16969, collection of J. Dwight. Examined by me July 20, 1933. Two labels attached; a third type label was added on this date by J. T. Zimmer. First, a small round label:

16969 | A B/$_{D}$ | Breeding | D; [reverse side] J. h. shufeldti | 14.5.06 ♂ | Okanagan.

Second (italics indicate print):

Collection of J. Dwight, Jr. | Junco hyemalis [*cancelled:* shufeldti$_{D}$] connectens ♂ | B. C., Okanagan May 14, 1906 | 16969 [vertically at right]; [reverse side] Like L. B. ♀ 4129 but paler | back blacker head. | A.M.N.H. | oreg.$_{D}$ [all in Dwight's hand, except A.M.N.H.].

Third, a pink American Museum type label:

Type of Junco oregonus couesi | Dwight.

Dwight (1918, p. 291) provided this name for birds that breed in the interior of British Columbia and in parts of both coastal and interior Washington and Oregon. He eliminated the name *shufeldti* by synonymizing it, incorrectly, with *oreganus,* whereas it can be applied to the coastal division of his *couesi.* He ruled out the name *montanus* because he believed it to represent a hybrid. An insufficient amount of breeding material made it impossible for Dwight to appreciate the variability of this race and hence the fact that the type and topotypes of *montanus* fit into the pattern of variation (see p.

392). *Couesi* as described, therefore, is a synonym partly of *shufeldti* and partly of *montanus,* but the type is an example of *montanus.*

The type has a back 2*b,* and head of about No. 4 intensity (see p. 247).

Type locality.—Okanagan, British Columbia.

Identification.—*Junco oreganus montanus.*

Junco hyemalis danbyi Coues

Coues did not name a type in the original description (1895, p. 14). Later he (1897, p. 94) states that the type was deposited in the United States National Museum, but does not give the number. This presumably is no. 153188, now labeled as the type, which I examined in July, 1933. Two labels are attached. First, a National Museum label from which the top part has been cut off:

Type specimen | No. [printed] Junco danbyi (=aikeni Sex. [printed] | Locality [printed] Custer City, So. Dak. Date [printed] Sept. 1895 Dr. E. Coues; [reverse blank].

Second, a National Museum–Smithsonian Institution type label:

53188 | Type of [printed] Junco danbyi Coues; [reverse blank].

The bird is typical of *aikeni;* the overcast plumage suggests that it is a female. The last primary is still in its sheath, indicating a primary molt which is just being completed. This means the bird is an adult, not a juvenile, or immature as Coues indicated. The absence of well-defined wing bars is not a constant sign of age; juveniles may show white spots on the coverts (see p. 347).

Measurements: wing, 87.7 mm.; tail, 79.0; bill length, 8.7; bill depth, 6.8; tarsus, 20.7; middle toe, 12.1; hind toe, 8.0. Tail pattern: rectrices five and six all white; outer web of fourth rectrix ¼ white, inner web ½ white; outer web of third black, inner web with white spot. The wing length is great for a female.

Type locality.—Custer City (Custer), Custer County, South Dakota. This is a breeding locality.

Identification.—*Junco aikeni.*

Junco phaeonotus colimae van Rossem

Type.—No. 99.2.1.2255, British Museum. Examined by me in 1934 before it was made a type. Sierra Nevada de Colima, Jalisco, Mexico, April 9, 1889; collected by W. B. Richardson.

Noted by me as possessed of characters average for *J. p. phaeonotus.*

Type locality.—Sierra Nevada de Colima, Jalisco, Mexico. The type probably was a breeding bird and almost certainly was on its breeding grounds.

Identification.—*Junco phaeonotus phaeonotus* (see p. 219). Original description by van Rossem (1938, p. 132).

Junco phaeonotus australis van Rossem

Type.—No. 99.2.1.2169, British Museum. Examined by me in 1934 before it was made a type. Omilteme, 8000 ft., Guerrero, Mexico, August 1, 1888; collected by Mrs. H. H. Smith.

Noted by me as possessed of characters average for *J. p. phaeonotus*.

Type locality.—Omilteme, 8000 ft., Guerrero, Mexico. This is a breeding station.

Identification.—*Junco phaeonotus phaeonotus* (see pp. 219–220). Original description by van Rossem (1938, p. 133).

APPENDIX B

BREEDING LOCALITIES

The localities listed in this appendix are those from which breeding or permanently resident birds have been examined. Only typical or unmixed populations are represented under a given name, unless otherwise stated.

Junco caniceps caniceps

COLORADO

Larimer County: Medicine Bow Range; Estes Park; Longs Peak.
Jackson County: Mount Zirkel; Hill Creek.
Routt County: Williams Range.
Boulder County: Boulder.
Grand County: Grandby.
Jefferson County: Golden; Wigwam Creek, near Deckers.
Gilpin County: Mount McClellan, Steven's Mill.
Clear Creek County: Alice; Berthoud's Pass.
Summit County: Breckenridge.
Eagle County: west slope Gore Range.
El Paso County: Pikes Peak; Mount Bross, near Alma; Montgomery; Fairplay; Bailey; South Park; Deer Creek; Elk Creek; Mount Ptarmigan.
Pueblo County: Beulah.
Fremont County: Sangre de Cristo Range.
Gunnison County: Cebolla.
Saguache County: upper Saguache River; Cochetopa Pass.
San Juan County: Silverton.
San Miguel County: Trout Lake; south fork of Rio San Miguel.
Dolores County: Rico.
Costello County: Fort Garland.
Conejos County: Osier.
Huerfano County: Wet Mountains.
Archuleta County: Little Navajo River; Pagosa.

NEW MEXICO

Colfax County: Taos Peak; Elizabethtown.
Taos County: 5 miles south of Twining.
Rio Arriba County: 8 to 12 miles north of El Rito.
San Miguel County: Pecos; Willis.
Santa Fe County: Pecos Forest Reservation; Pecos Baldy.
Sandoval County: James Mountains, 25 miles west of Española.
McKinley County: Chuska Mountains, Long Lake, 8800 feet.

UTAH

Summit County: 10 miles east of Kamas; Mount Baldy.
Sanpete County: Great Basin Experiment Station east of Ephraim.
Sevier County: 10 miles north of Fish Lake.
Garfield County: 7 miles east of Widtsoe.
Iron County: Cedar Breaks.
San Juan County: Navajo Mountain.

NEVADA

Humboldt County: Martin Creek Ranger Station, 7000 feet, Santa Rosa Mountains.
Elko County: Secret Pass; Three Lakes; south fork of Long Creek (all in Ruby Mountains).
White Pine County: Lehman Creek and Baker Creek, Snake Mountains; Cleve Creek,

Shell Creek Range; 3 miles west of Hamilton, White Pine Mountains; Hendry Creek, 9100 feet, 1½ miles east of Mount Moriah.

Eureka County: 4 miles south of Tonkin, Denay Creek, Roberts Mountains.

Lander County: Birch Creek and Kingston Creek, Toyabe Mountains; Peterson Creek, Shoshone Mountains.

Nye County: Green Monster Cañon, Monitor Range; north slope of Toquima Peak; head of Reese River, Arc Dome, Mohawk Ranger Station, Wisconsin Creek, north of Twin River and South Twin River in Toyabe Mountains.

Lincoln County: Wilson Peak [Cedar Range], 8500 feet.

Intermediates (hybrids) between *J. c. caniceps* and *J. c. dorsalis*

ARIZONA

Coconino County: Bright Angel; 1 mile north of National Park Boundary, Kaibab Forest; 2–3 miles west of V. T. Ranger Station; 3 miles south of Dry Park Ranger Station; 4 miles north of Jacob's Lake (all on Kaibab Plateau).

NEW MEXICO

Valencia County: Bear Ridge, Zuni Mountains; San Mateo Mountains (probably hybrid population).

McKinley County: Nutria, Zuni Mountains.

Intermediates (hybrids) between *J. c. caniceps* and *J. o. thurberi*

NEVADA

Clark County: Lee Cañon, 8200 to 9200 feet; Clark Cañon, Charleston Park, and north base of Charleston Peak, Charleston Mountains; Hidden Forest, 8500 feet, Sheep Mountains.

Nye County: Grapevine Peak, 8000–8500 feet; 2½ miles east, 1 mile south of Grapevine Peak, 6700 feet.

Esmeralda County: Chiatovich Creek, 8000 to 8200 feet, and Quinn Mine, 10,000 feet, White Mountains.

Mineral County: 2 miles southwest of Pine Grove, 7250 feet; Cottonwood Creek, 7900 feet; Lapon Cañon, 8900 feet; south fork of Cat Creek, 8500 feet.

Douglas County: Desert Creek, 7100 feet, Sweetwater Range.

Humboldt County: Duffer Peak, 8400 feet, Pine Forest Mountains.

CALIFORNIA

San Bernardino County: northwest side Clark Mountain, 7300 feet.

Inyo County: Mountain Spring Canyon, 6600 feet, Argus Mountains; Hanaupah Canyon, 9300 feet, and "Coalkilns" [Wildrose Canyon], Panamint Mountains; head of Lead Cañon, 10,000 feet, Inyo Mountains; Weyman Creek, 8200 feet, White Mountains.

Mono County: McAfee Creek, 10,000 feet; near Blanco Mountain, 10,500 feet; near Big Prospector Meadow, 10,300 feet; Poison Creek, 9600 feet; McCloud Camp on Cottonwood Creek, 9200 feet (all in White Mountains).

Intermediates (hybrids) between *J. c. caniceps* and *J. o. mearnsi*

WYOMING

Albany County: Laramie Peak, 10,000 feet.

Carbon County: south base of Bridger Peak, 8800 feet, Sierra Madre Mountains; Black Hills [=Medicine Bow Range].

Natrona County: Rattlesnake Mountains, 7500 feet; Casper Mountains.

Uintah County: Camp Scott, Fort Bridger.

UTAH

Cache County: 12 miles west of Garden City.

Rich County: 8 miles west of Randolph; 14 miles southwest of Woodruff.

Weber County: Beaver Canyon, 7500 feet [Beaver River].

Summit County: Porcupine Ridge near Upton.

IDAHO

Bannock County: Swan Lake.

Cassia County: Albion; Mount Harrison, 10 miles south of Albion; 8 miles southwest of Elba.

NEVADA

Elko County: summit between Copper and Coon creeks, Jarbidge Mountains.

Humboldt County: Duffer Peak, 8400 feet, Pine Forest Mountains.

Junco caniceps dorsalis

TEXAS

Culberson County: Guadalupe Mountains.

NEW MEXICO

Lincoln County: Alto; southwest slope of Capitan Mountains; south branch of Carrizo Creek, near foot of Sierra Blanca Peak, 7600 feet.

Otero County: Tularosa Canyon, 6850 feet, 4 miles above Mescalero; Cloudcroft.

Socorro County: head of Water Canyon, 9300 feet, Magdalena Mountains.

Catron County: 8 miles southeast of Mogollon.

Grant County: Head of Mimbres [River]; Big Rocky Creek, 8000 feet.

ARIZONA

Greenlee County: Hannagan Meadow.

Apache County: 7 miles north of Big Lake; Marsh Lake [Big Lake]; Horseshoe Cienega; Willow Springs; summit of White Mountains; Cooley [McNary]; 6 miles south-southwest of Greer; Odart Mountain, 8300 feet; PS Ranch, 28 miles south of Springerville.

Navajo County: Apache [Fort Apache].

Gila County: Aztec Peak, Sierra Ancha.

Coconino County: Baker's Butte; Pivot Rock Spring; 3 miles southwest of Long Valley; Little Spring, north side of San Francisco Mountain; San Francisco Mountain; 8 miles north of Maine [Sitgreaves Mountain]; Williams.

Yavapai County: Mingus Mountain; Mount Union, Bradshaw Mountains; Mount Francis, 6500 feet, Prescott.

Junco phaeonotus palliatus

NEW MEXICO

Hidalgo [formerly Grant] County: Animas Peak, 8000 feet; Summit of San Luis Mountains; Big Hachita Mountain.

ARIZONA

Gila County: Pinal Mountain, 7500 feet.

Graham County: Graham [Pinalino Mountains], 8400–9200 feet; Mount Graham.

Pinal County: Santa Catalina Mountains: Catalina Mill; [San] Pedro slope; 4000 feet.

Pima County: Santa Catalina Mountains: Soldier's Camp, 7700 feet; Mount Bigelow, 8300 feet.

Cochise County: Chiricahua Mountains: Pinery Canyon, 6000–7000 feet; Ida Peak, 8000 feet; Rustler Park, 8700 feet; Bar Foot Park, 8300 feet; Paradise, 6000 feet; Flys Peak, 9500 feet; Monte Vista, 8000 feet. Whetstone Mountains. Huachuca Mountains: 7000–8500 feet; Palmerlee; head of Miller Canyon, 8400 feet; Ramsay Canyon, 9000 feet.

Santa Cruz County: Santa Rita Mountains: Madera Canyon, 4700 feet; Stone Cabin Canyon, 8500 feet.

MEXICO

Sonora: San José Mountains.

Chihuahua: San Luis Mountains; Colonia Juárez; near Colonia Garcia; Water Cañon, 7200 feet, 3 miles south of Colonia Garcia; 9 miles southeast of Colonia Garcia, 8200 feet; Pachaco [= Pacheco]; Chuchuichupa [= Chuhuichupa and Chuichupa]; Bustillos; 30 miles west of Miñaca; Jesús María; Pinos Altos; El Carmén; Rio Verde, 8000 feet.

Localities in intergradient areas in central Mexico between *J. p. palliatus* and *J. p. phaeonotus*

MEXICO

Coahuila: Sierra Encarnación [20 miles southwest of Carneros]; Sierra Guadalupe [20 miles southwest of Saltillo].

Durango: Arroyo de Buey, 7500 feet [northwest Durango]; El Salto; Ciudad Durango.

Tamaulipas: Miquihuana; Ciudad Victoria; Galindo.

Nuevo León (no specific locality).

San Luis Potosí: Sierra de San Luis Potosí; mountains 25 miles west of Charcas, 7000–8000 feet; mountains near Jesús María.

Zacatecas: Jérez; Sierra Valparaíso.

Aguascalientes: Sierra de Aguascalientes.

Jalisco (northern): Bolaños; Sierra Bolaños; Sierra Nayarit, 8000 feet.

Nayarit (Tepic): Sierra Madre.

Junco phaeonotus phaeonotus

MEXICO

Vera Cruz: Las Vigas, 8000 feet; Coatepec; Jalapa; Jico [= Xico]; Perote; Mirador.

Pueblo: Chalchicomula, 8700 feet; Pine Forest, 10,000 feet, Mount Orizaba; Chachapa; Pinal.

Tlaxcala: Maquey Verde, 7100 feet, 8½ miles northeast of Zimapan; Mount Malinchi.

Hidalgo: Real del Monte; El Chico.

Mexico and Federal District: Rio Frio, Ixtaccihuatl; Amecameca; Popocatepetl, 12,000 feet; Tenango; City of Mexico [probably vicinity of]; Coajimalpa and Chimalpu, vicinity of Tacubaya; Culhuacán, Mexicalcingo, and Hacienda Eclava, vicinity of Tlalpam; Salazar; Las Cruces, Valley of Mexico; Tetalco, vicinity of Xochimilco; Ajusco; north slope of Volcán Toluca.

Michoacán: Pátzcuaro; Nahuatzen; Patambán.

Jalisco (southern): Sierra Nevada de Colima; Volcán de Nieve, 10,000–14,000 feet, Sierra Nevada de Colima; Juanacatlán.

Guerrero: Omilteme, 8000 feet.

Oaxaca: Villa Alta; Tonagnia; Totontepec; Mount Zempoaltepec.

Junco bairdi

MEXICO

Lower California. Cape Region: Sierra de la Laguna (Sierra Laguna); Victoria Mountains; La Laguna; Laguna Valley; El Sáuz (also El Sauce); 14 miles northwest of San Bernardo; Mount Miraflores.

Junco fulvescens

MEXICO

Chiapas: San Cristóbal; Teopisca.

Junco alticola

GUATEMALA

Amatitlán (Department of): Volcán de Agua.

Sacatepéquez: Volcán de Fuego, 10,200–12,000 feet, pine forests.

Chimaltenango: Tecpam, 9500 feet; Santa Llana, 10,000 feet (about six miles from Tecpam).

Solola: San José Solola, 8000 feet.

Quezaltenango: Quezaltenango [7700 feet]; Chuipaché; San Martín; Volcán Santa María; Calel.

San Marcos: San Marcos [8000 feet]; Tajumulco, 10,500 feet; Zanjón (9500 feet).

Totonicapán: Momostenango [6500 feet]; Totonicapán [8000 feet].

El Quiché: Chichicastenango [6500 feet].

Huehuetenango: San Mateo [9000 feet]; Hacienda Chancol, 11,000 feet [=Chancol]; Todos Santos.

MEXICO

Chiapas: Volcán Tacaná, 11,000 feet; Niquivil [or Niquihuil]; Chiquihuite, 8200 feet.

Junco vulcani

COSTA RICA

Volcán Irazú [various slopes of mountain]; Volcán Turrialba, 8500–11,000 feet; Las Vueltas [Dota Mountains].

PANAMA

Volcán Chiriquí, 11,000–11,200 feet.

Junco oreganus mearnsi

SASKATCHEWAN

Maple Creek District: Cypress Hills near Maple Creek.

ALBERTA

Medicine Hat District: Eagle Butte.

MONTANA

Garfield County: 20 miles west of Lismas [possibly in Valley County].

Phillips County: Ruby Creek, Zortman, Little Rocky Mountains.

Fergus County: 15 miles south of Heath, Big Snowy Mountains; 5 miles northwest of Hilger.

Judith Basin County: Buffalo Canyon, 13 miles west of Buffalo; Dry Wolf Creek, 20 miles southwest of Stanford, Little Belt River Mountains.

Cascade County: Belt River Canyon [Belt Creek].

Meagher County: Sheep Creek, 16 miles north of White Sulphur Springs, Little Belt Mountains.

Musselshell County: 16 miles south of Roundup.

Sweetgrass County: 14 miles south of Big Timber; head of Timber Creek, Crazy Mountains.

Gallatin County: Mystic Lake [20 miles south of Bozeman]; west fork of West Gallatin River, 6500 feet.

Madison County: Ward Peak, Washington Creek, 6500 feet.

Big Horn County: Lodgegrass Creek, 8000 feet, Big Horn Mountains.

WYOMING

Sheridan County: Big Horn Mountains near Sheridan.

Big Horn County: head of Trapper's Creek, west slope of Big Horn Mountains, 5500–8500 feet.

Park County: northeast base of Black Mountain; Whirlwind Peak; Grinnett Creek near Pahaska Tepee; Pahaska [=Pahaska Tepee]; 12 miles north of Wapiti; Valley; Needle Mountain.

Yellowstone Park: Lower Geyser Basin.

Fremont County: Whisky Mountain, 5 miles south of Dubois, 10,000 feet; Bull Lake.

Teton County: south of Moose Creek, 10,000 feet, Teton Mountains.

Sublette County: Kendall; 12 miles north of Kendall, 7700 feet; 7 miles south of Fremont Peak, 10,400 feet; 5 miles northwest of Merna, 8500 feet; 1 mile north of Green River Lakes, 8300 feet.

Lincoln County: Head of Dry Creek, Salt River Mountains, 9200 feet.

IDAHO

Custer County: head of Pahsimeroi River.

Fremont County: Mack's Inn near Trude; 17 miles east, 4 miles north of Ashton, 6275 feet.

Teton County: 3 miles southwest of Victor.

Bonneville County: Big Hole Mountains, 8 miles northeast of Swan Valley.

Bannock County: Inkom.

Bear Lake County: west rim of Copenhagen Basin, 8400 feet, Wasatch Mountains.

Franklin County: 20 miles northeast of Preston, Strawberry Creek, 6700 feet.

Intermediates between *J. o. mearnsi* and *J. o. montanus*

MONTANA

Deer Lodge County.

IDAHO

Custer County: Mill Creek, 14 miles west-southwest of Challis, 8370 feet; Stanley Lake; 5 miles west of Cape Horn, Sawtooth Mountains.

Blaine County: Alturas Lake.

Valley County: 5 miles east of Warm Lake; Lardo (nearly typical *montanus* population).

Adams County: 3 miles west of Payette Lake (nearly typical *montanus*).

Boise County: Idaho City.

Junco oreganus montanus

Breeding localities at which there are relatively unmixed populations. Where mixture with *J. hyemalis* is known, the locality is marked with an asterisk.

BRITISH COLUMBIA (districts as indicated in Rand McNally Commercial Atlas of 1934)

Skeena District: Kispiox Valley,* 23 miles north of Hazelton; Nine-Mile Mountain,* 20 miles northeast of Hazelton, 4000 feet; Hazelton, 959 feet; New Hazelton; Driftwood River, 15 miles northwest of Tacla Lake; 10 miles west of Tacla Lake, Babine Trail; 15 miles east of Babine; Telkwa.

Cariboo District: Stuart Lake; Vanderhoof; mouth of Big Salmon River [= McGregor River]; Cottonwood;* Indianpoint Lake;* Isaac Lake; 3 miles east of Moose Lake (probably mixture); north fork, and mouth, of Moose River (probably mixture); Yellowhead Lake;* Yellowhead Pass;* Moose Pass;* Kleena Kleene; 15 miles southwest of Kleena Kleene; 5 miles northwest of Redstone; Alexis Lake; 20 miles south of Chezacut; 150 Mile House; Lac la Hache; Clearwater; 12 miles north of Clearwater;* Grizzly Peak, 10 miles west of Clearwater; Sicamous; Ducks; Revelstoke; Ashcroft; 12 miles north of Clinton; Lillooet.

West Kootenay District: Summit [= Summit Lake?]; Deer Park, Lower Arrow Lake; Nelson; Rossland;* Trail; Creston.*

East Kootenay: Glacier; Field;* Cranbrook.*

Yale District: Okanagan; Okanagan Landing; Shuswap Falls; Vaseaux Lake, Okanagan Valley; Inkaneep Creek, Okanagan Valley; Midway.

Alberta (all localities in regions of considerable intermixture): Henry House; 15 miles south of Henry House; Fork of Blindman and Red Deer rivers; Red Deer River at Didsbury; Banff.

WASHINGTON

Okanagan County: Tunk Mountain.

Columbia County: 21 miles southeast of Dayton, east fork of Touchet River, Blue Mountains.

Asotin County: Anatone, Blue Mountains, 3500 feet; 15 miles north of Paradise [Oregon] at Horse Creek, 2000 feet.

IDAHO

Boundary County: 4 miles west of Meadow Creek, 3000 feet.

Bonner County: 5 miles west of Cocolalla, 3000 feet.

Kootenai County: 5 miles north of Coeur d'Alene; Fernan Hill, Coeur d'Alene.

Shoshone County: Thompson Pass; Glidden Lakes, 5700 feet.

Clearwater County: 2 miles northeast of Weippe, 3000 feet.

Idaho County: Castle Creek Ranger Station, south fork of Clearwater River, 1800 feet.

Adams County: 1 mile north of Bear Ranger Station, southwest slope of Smith Mountain, 5400 feet; Thorn Creek Ranger Station, 3 miles west of Payette Lake, 5400 feet (nearly typical *montanus*).

Valley County: Lardo (nearly typical *montanus*).

Washington County: 1 mile northeast of Heath, southwest slope of Cuddy Mountain, 4000–4600 feet.

MONTANA

Lincoln County: Tobacco Plains [=Tobacco].

Flathead County: Columbia Falls; Flathead Lake.

Glacier County: Saint Mary's Lake.

Sanders County: Thompson Falls.

Missoula County: Lolo Creek, 3470 feet, 6½ miles west of Lolo (nearly typical *montanus*).

Ravalli County: Florence, west of, 7300 feet (nearly typical *montanus*).

OREGON

Jefferson County: Haycreek, 12 miles east of Foley Creek.

Crook County: Ochoco Ranger Station, 4000 feet; Howard; Maury Mountains.

Grant County: John Day River; Beech Creek; Strawberry Mountains; 12 miles south of Canyon City, 5500 feet; Cold Spring, 4900 feet, 8 miles east of Austin.

Umatilla County: Meacham.

Wallowa County: Billy Meadows Ranger Station.

Union County: Elgin; Catherine Creek, 7 miles northeast of Telocaset, 3500 feet.

Baker County: Homestead, 3500 feet; Bourne; McEwen; Home, 3000 feet.

Intermediates between *J. o. shufeldti* and *J. o. montanus*

OREGON

Deschutes County: Lapine; Paulina Lake; 3 miles west Paulina Lake; 1 mile south East Lake, Paulina Mountains.

Junco oreganus shufeldti

BRITISH COLUMBIA (extreme southwestern mainland)

Desolation Lake, Howe Sound; Brackendale, Howe Sound; Seymour Mountain; New Westminster; Port Moody; Mount Lehman; Chilliwack; Agassiz; Sumas.

WASHINGTON

Whatcom County: 35 miles east of Glacier, 3500 feet; Bonita Mine, Barron, 6000 feet; Lummi Island.

Okanagan County: Hidden Lakes, 4100 feet; Mazama, 2100 feet; west fork of Pasayten River, 4700 feet, at mouth of Holman Creek.

Skagit County: Mount Vernon.

Chelan County: Railroad Creek, 3900 feet, Hart Lake; Tyee Peak, 3000–5000 feet, Entiat; Stormy Peak, 5500 feet, near Entiat; Wenatchee Lake, 1870 feet.

King County: Kirkland; Seattle; Redmond.

Pierce County: Tacoma; Indian Henry's Ranger Station, 5300 feet, Mount Rainier; above Paradise Park, 6500 feet, Mount Rainier.

Lewis County: Reflection Lakes, 4900 feet, Mount Rainier; Stevens Creek, 3000 feet, Mount Rainier.

Clallam County: 2 miles southwest of Mount Angeles, 6000 feet; head of Little Creek, 5000 feet, Mount Angeles; Cañon Creek; 3 miles south of Soleduck [Sol Duc] River, 3550 feet; Lake Sutherland, 500 feet; mouth of Boulder Creek, 560 feet, Elwha River, Olympic Mountains; Happy Lake, 4900 feet; Frazier Creek, 800 feet, 4 miles southwest of Port Angeles.

Jefferson County: Port Townsend; Elwha Basin, Elwha River, 2750 feet; upper Quinault.

Grays Harbor County: Quinault Lake.

Thurston County: Tenino.

Yakima County: Gotchen Creek, 4000 feet, Mount Adams; Signal Peak.

Wahkiakum County: 4 miles east of Skamokawa.

Clark County: Vancouver.

Skamania County: Mount Saint Helens; 60 miles east by trail from Toledo [Lewis County].

Klickitat County: Grand Dalles.

OREGON

Tillamook County: Netarts; Mount Hebo, 3165 feet; Tillamook.

Washington County: Forest Grove; Beaverton.

Multnomah County: Portland.

Marion County: Salem.

Jefferson County: Mill Creek, 20 miles west of Warm Springs.

Linn County: Lookout Mountain.

Lane County: Eugene; McKenzie Bridge.

Deschutes County: Sisters; 16 miles west of Bend, 6500 feet.

Coos County: Lakeside; 3 miles south of Cape Arago; 2 miles north of Bandon.

Intermediates between *J. o. oreganus* and *J. o. shufeldti*

BRITISH COLUMBIA

Calvert Island (nearest *oreganus*): Johnstone Strait; Lund. Vancouver Island: Mount Arrowsmith; Halls Ranch, Alberni Valley; Errington; Golden Eagle Mine, 18 miles south of Alberni; Great Central Lake; Little Qualicum River.

Junco oreganus oreganus

ALASKA

Yakutat; Glacier Bay; Gustavus Point, Glacier Bay; Haines; Port Frederick; Kelp Bay [Baranof Island]; Red Bluff Bay, Baranof Island; Hooniah Sound; Sitka; Old Sitka; Taku River; Port Snettisham; Windfall Harbor; Mole Harbor; Farragut Bay; Thomas Bay; Petersburg, Mitkof Island; St. John Harbor, Zarembo Island; Kasaan Bay, Prince of Wales Island; Three Mile Arm, Kuiu Island; east end of Heceta Island; east side of Warren Island; Rocky Bay, northwest Dall Island; Wrangell; Etolin Island; Portage Cove, Revillagigedo Island; Ketchikan.

BRITISH COLUMBIA

Fort [Port] Simpson. Queen Charlotte Islands: McIntosh Meadows near Massett; Massett; Langara Island; Cumshewa Inlet. Yule Lake, Swanson Bay; "Soda Creek," 52° 47′ N, 128° 33′ W, Princess Royal Island; Borrowman Bay, Aristazabl Island.

Intermediates between *J. o. oreganus* and *J. o. montanus*

BRITISH COLUMBIA

Bella Coola, 5000 feet; 13 miles east of Bella Coola; 18 miles east of Bella Coola (intermediates). Thirty miles east of Bella Coola; Cariboo Mountain, 5000 feet, Stuie [Bella Coola Valley]; Plateau above Hotnarko River, 2–4 miles east of Precipice; Anahim Lake; Rainbow Mountains (all nearest *montanus*). Peak above Swanson Bay (near *oreganus*)

Intermediates (hybrids) between *J. o. oreganus* and *J. h. cismontanus*

ALASKA

Glacier, White Pass; Bradfield Canal.

BRITISH COLUMBIA

Flood Glacier, Stikine River; Great Glacier (chiefly *oreganus*), Stikine River.

Intermediates between *J. o. shufeldti* and *J. o. thurberi*

(Principal regions of intergradation)

OREGON

Curry County: Port Orford.

Douglas County: Reston; Lookingglass; Drew; Minnehaha Creek, Diamond Lake Road, Crater Lake National Forest; 5 miles south Mount Thielsen.

Josephine County: Grants Pass; Onion Mountain Lookout.

Jackson County: Trail; Prospect.

Klamath County: Crater Lake; Anna Springs [Crater Lake National Park]; Fort Klamath; Algoma; Swan Lake Valley.

Junco oreganus thurberi

OREGON (many somewhat intermediate toward *shufeldti*)

Josephine County: Lind Home, 5 miles north-northeast of Holland; junction of Grayback and Sucker creeks; 5 miles northwest of Bolan Lake.

Jackson County: Siskiyou; Siskiyou Mountains; Colestin; north base of Ashland Peak, 4000 feet.

Klamath County: Bonanza.

Lake County: 3 miles east of Lakeview, 5400 feet; north base of Crook Peak, Warner Mountains; Fort Warner, Hart Mountains; Barley Camp, 14 miles southwest of Adel.

CALIFORNIA

Del Norte County: 7 miles east-northeast of Smith River, 1800 feet; Bald Hill, 9 miles east of Crescent City; Patrick's Creek; east fork of Illinois River, 1900 feet, ¼ mile south of Oregon line.

Siskiyou County: Poker Flat, 5000 feet, 12 miles northwest, and 9 miles west, of Happy Camp; Bald Mountain; head of Doggett Creek, 5800 feet, Siskiyou Mountains; west fork of Cottonwood Creek, 4000 feet, 4½ miles southwest of Hilt; Old Piney Mine, 4 miles southwest of Greenview; Salmon Mountains near Greenview; Fort Jones; Forest House Mountain, 8 miles west of Yreka; Vernon Mine near Yreka; Jackson Lake, 5900 feet; south fork of Salmon River, 5000 feet; head of Rush Creek, 6400 feet; Kangaroo Creek; Castle Lake, 5434 feet; Bray; Goose Nest Mountain; Mount Shasta, 7500 feet; head of Squaw Creek, 7600 feet, Mount Shasta; timber line, Mud Creek, Mount Shasta; Horse Camp, 7200 feet, Mount Shasta; Sisson; Bear Creek; Weed; Stewart Springs near Weed; T. H. Benton estate, Butte Creek; McCloud.

Modoc County: Camp [Fort] Bidwell; Lake City; Cedarville; head of north fork of Parker Creek, 7300 feet, Parker Creek 5500 feet, middle fork of Parker Creek, 7500 feet, and head of Dry Creek, 7000 feet, Warner Mountains; east face of Warner Peak; Eagleville; near Willow Ranch; Sugar Hill, 5000–6000 feet; near Davis Creek, Sugar Hill, 5500 feet.

Humboldt County: 8–12 miles east of Arcata, 1200 feet; Hoopa Valley; Coyote Peak, 3000 feet; Horse Mountain, 4700–5200 feet; South Fork Mountain, 5500–5700 feet, near Blake Lookout; 4 miles northeast of Bridgeville, 1800 feet, McLellan Ranch; forks of Van Deuzen River, 8 miles east of Bridgeville; 10 miles north of Garberville.

Trinity County: Norgaar's Ranch, 2000 feet, South Fork, Trinity River; summit of South Fork Mountains, 3 miles east of Forest Glen; 4–10 miles northwest of Forest Glen, 3100–3600 feet; Salyer; Peanut; Mad River Ford, 2700 feet, above Ruth; Bully Choop Mountains, 20 miles east of Weaverville; head of Grizzly Creek, 6000 feet; north fork of Coffee

Creek, 4500 feet; head of Bear Creek, 6400 feet; divide, 12 miles north of North Yolla Bolly Mountain.

Shasta County: 3 miles west of Knob; Lake Helen, 8500 feet, south base of Lassen Peak; Manzanita Lake, 6000 feet; Burney.

Tehama County: ½ mile to 2 miles south of South Yolla Bolly Mountain; Lyonsville; 5 miles northwest of Lyonsville; 2 miles west of Black Butte, 6800 feet; Round Valley Ranger Station; Mineral, 6000 feet.

Lassen County: Hayden Hill; Mount Lassen; southeast side of Lassen Peak; Mill Creek, south base of Mount Lassen; Bogard Ranger Station; Honey Lake; Eagle Lake.

Mendocino County: 3 miles south of Covelo; Cahto; Laytonville; Sherwoods; 14 and 22 miles west [by road] of Willets; Mount Anthony; 4500 feet, 6000 feet, and 3 miles west of summit of Mount Sanhedrin; Mendocino City, 75 feet; Ornbaun Post Office; 5 miles west of Ornbaun Spring.

Lake County: Glenbrook, Cobb Post Office.

Colusa County: Fout's Springs; Snow Mountain.

Napa County: Mount Saint Helena.

Sonoma County: Gualala River; Gualala, 50 feet; Sea View; 7 miles west of Cazadero.

Butte County: Jonesville; Magalia.

Plumas County: Mohawk; Quincy; Meadow Valley; Johnsville; Lights Cañon.

Sierra County: Sierra City, 6800 feet; Sierraville, 5300–5500 feet.

Nevada County: Independence Lake.

Placer County: Blue Cañon; Emigrant Gap; Cisco; Donner, 7900 feet; Squaw Valley near Truckee; Tahoe Tavern.

El Dorado County: Placerville; Fyffe, 3500–4000 feet; Kyburz; Pyramid Peak; Glen Alpine; Mount Tallac; Echo, 7000 feet; Summit of Tahoe-Placerville Road; Meyers, Lake Tahoe.

Alpine County: 3 miles south-southwest of Woodfords, 7800 feet.

Calaveras County: Big Trees.

Tuolumne County: Stanislaus River, 4600–5000 feet; head of Lyell Canyon, 9700 feet.

Mariposa County: near Porcupine Flat, 8100 feet; east fork of Indian Canyon, 7300 feet; 1 mile east of Merced Lake; near Mono Meadow, 7300 feet; Yosemite Valley; Merced Grove of Big Trees, 5500 feet; Dudley, 3000 feet; 5 miles northeast of Coulterville, 3200 feet.

Mono County: Warren Mountain, 10,000 feet, near Mono Lake; Parker Creek, 7500 feet; near Walker Lake, 8000 feet; Mammoth Lakes.

Fresno County: south fork of San Joaquin River at Evolution Creek junction, 8500 feet; Bubb's Creek Cañon; Hume; Bullfrog Lake, 10,000 feet; Horse Corral Meadows.

Tulare County: Whitney Meadow, 9800 feet; Taylor Meadow, 7000 feet; Whitney Creek, 11,000 feet; Mount Whitney; Monache Meadow, 8000 feet; Jackass Meadow, 7750 feet; Sirretta Meadow, 9000 feet; Olancha Peak, 10,000 feet; Coyote Creek, east side of summit of Western Divide; east fork of Kaweah River, 9700 feet; Sequoia Park; North Tule; Weisher's Mill [6000 feet, east fork of Kaweah River].

Inyo County: Owens Valley; Onion Valley, 8500 feet, and Flower Lake [= Heart Lake], 10,500 feet, Kearsarge Pass; Cottonwood Lakes, 11,000 feet; Little Cottonwood Creek, 9800 feet.

Kern County: Kiavah Mountain, 6000–7000 feet near Walker Pass; Mount Breckenridge, 6000 feet, 12 miles below Bodfish; Piute Mountains; Fort Tejon; northeast side of Mount Pinos.

Ventura County: Mount Pinos, 8500 feet.

Los Angeles County: Arroyo Seco Canyon, near Pasadena; Buckhorn; Pine Flats; Chileo; Wilson's Peak [= Mount Wilson]; Strain's Camp; West Fork [San Gabriel River] near [?] Pasadena (all in San Gabriel Mountains).

San Bernardino County: Bear Valley; Bluff Lake, 7400 feet; Fish Creek, 6500 feet; south fork of Santa Ana River, 6200–8500 feet; Sugarloaf, 8000–9000 feet; Santa Ana

[River], 5500–6600 feet; San Bernardino Peak; Lost Creek, 6400 feet; Oak Glen; San Gorgonio Peak, 11,500 feet (all in San Bernardino Mountains).

Riverside County: near Beaumont; Round Valley, 9000 feet; Fuller's Mill, 5900–6000 feet; New Mill Site, near Fuller's Mill, 5300 feet; Tahquitz Valley, 8000 feet; Thomas Mountain, 6800 feet; Strawberry Valley, 6000 feet (all in the San Jacinto Mountains). Garnet Queen Mine, 6000 feet; Toro Peak, 8000 feet; Santa Rosa Peak, 7500 feet (all in the Santa Rosa Mountains).

Orange County: Los Pinos Peak, 4000 feet, Santa Ana Mountains.

San Diego County: Julian; Campbell's Ranch, Laguna Mountains; Laguna; Cuyamaca Mountain; Volcan Mountain; Volcan; Smith Mountain [Palomar Mountain].

NEVADA (typical populations only)

Washoe County: Galena Creek, 7000–8000 feet.

Douglas County: Glenbrook.

Intermediates between *J. o. thurberi* and *J. o. pinosus*

CALIFORNIA

Marin County: Inverness; San Geronimo; San Rafael.

San Luis Obispo County: Santa Margarita, 996 feet; Salinas River, 1000 feet, 3 miles northeast of Santa Margarita (closer to *pinosus* than to *thurberi*); 4 miles west of La Panza.

Junco oreganus pinosus

CALIFORNIA

Alameda County: Strawberry Canyon and University of California campus, Berkeley.

Santa Clara County: east side of Mount Hamilton; Alma.

San Mateo County: King Mountain; Pescadero; Pescadero Creek Basin; Butano Basin.

Santa Cruz County: Santa Cruz Mountains, 2300 feet; summit between Los Gatos and Boulder, Santa Cruz Mountains; Big Trees; Boulder Creek; Santa Cruz; 2½ miles east, 1 mile north-northeast of Santa Cruz, 300 feet.

San Benito County: Big Oak Flat, 3300 feet, 4 miles northeast of San Benito; Butts Ranch, 3000 feet, 5 miles north-northeast of San Benito; summit, 5250 feet, and 1 mile southeast of summit, 4400 feet, San Benito Mountain; Laguna Ranch, 4000 feet, 4 miles south of Hernandez.

Monterey County: Monterey; Pacific Grove; Point Pinos; Garrapatos Creek; Little Sur River; head of Turner Creek, 2700 feet; Big Pines, 3500–3700 feet [=The Pines and Government Camp, Danish Creek]; Big Sur River; Lucia P. O., headwaters of Big Creek; Santa Lucia Peak, 5600 feet; 6 miles below Tassajara Springs, Tassajara Creek; Partington Point, 1¼–2 miles south of Chalk Peak, 3000 feet.

Junco oreganus pontilis

MEXICO

Lower California. Sierra Juárez: Laguna Hanson; El Rayo.

Junco oreganus townsendi

MEXICO

Lower California. Sierra San Pedro Mártir: San Pedro Mártir Mountain, 7500–8500 feet; Concepción, 6000 feet (November); La Joya, 6200 feet (October); Vallecitos, 7500–8500 feet; La Grulla, 7200–7500 feet; Santa Rosa Flats (6000 feet).

Junco insularis

MEXICO

Lower California. Guadalupe Island, sea level to 3500 feet.

Junco hyemalis hyemalis

ALASKA

Point Barrow; Wainwright; Kowak River; Cape Prince of Wales; Wales; Cairn, Norton Sound; north fork of Kuskokwim River, base of Mount Sischu; Dry Creek, 2600 feet, and Savage River, 2800 feet, Mount McKinley district; Sheep Creek [of Talkeetna Mountains?]; Lake Clark; Iliamna Village, Lake Iliamna; Knik River, Cook Inlet; Hope; Kenai Mountains; Seward; Homer; Seldovia; head of Port Nell [Nellie] Juan and head of Cordova Bay, Prince William Sound; Circle; Yukon River, 20 miles above Circle; Charlie Creek [= Kandik River]; mountains near Eagle; Rapids; Tanana Crossing.

YUKON

Forty-mile; Chandindu River, Yukon River; Dawson; White River, Yukon River; Russell Mountains, near forks of Macmillan River.

MACKENZIE

Fort Good Hope, Mackenzie River; Great Bear River; Fort Simpson; Willow River near Fort Providence; Hay River; Great Slave Lake; Fort Resolution; Great Slave River; Maufelly Point, Taltheilei Narrows and Belle Isle, Charlton Bay, Great Slave Lake.

ALBERTA

Bon Accord; Hastings Lake; Athabasca River; Fort Smith; Fort Chipewyan; Cypress Point and 10 miles northeast of Sand Point, Lake Athabasca.

SASKATCHEWAN

Lake Athabasca: 8 miles northeast of Moose Island, mouth of Beaver River, and north shore.

MANITOBA

Churchill; Norway House; Oxford.

ONTARIO

Moose Factory; East Point, James Bay; Cochrane; Dane; New Liskeard; Brunswick House [New Brunswick]; G. T. P. Crossing [=Mattice]; Coboconk.

QUEBEC

Richmond Gulf; Cairn Island, Richmond Gulf; James Bay; Great Whale River, James Bay; Aquatuk Bay; East Main, James Bay; Fort George, James Bay; Charlton Island, James Bay; Rupert House; Tadousac; Point Natashquan; mouth of Necatina [=Mekattina] River; Ste. Margaret [Margarite] River; Fauriel, Grosse Isle, Magdalen Islands.

NEWFOUNDLAND LABRADOR

Tikkoatokok Bay; Nain; Groswater Bay [= Lake Molville]; Lanc au Loup [= L'Anse au Loup, Loup Bay].

NEWFOUNDLAND

Bay of Islands; Port-au-Port; Spruce Brook; Nicholasville.

PRINCE EDWARD ISLAND

Tignish; Summerside; Souris.

NEW BRUNSWICK

Bathurst; Salisbury; Hillsborough; Hampton; Rothsay; Point Lepreaux; Grand Manan.

NOVA SCOTIA

Kelly's Cove, Cape Breton Island; Plaster Cove, Strait of Canso; Whycocomagh; Sable Island; New Port; Barrington; Cape Sable Island.

WISCONSIN

Oneida County: Woodruff.

Dodge County: Beaver Dam (May 25, breeding?).

NEW YORK (somewhat intermediate)
Franklin County: Chateaugay; St. Regis Lake.
Lewis County: Locustgrove.
Herkimer County: Fulton Chain Lakes.
Essex County: Keene.
Rensselaer County: Berlin.
Greene County: Hunter Mountain; High Peak, 3800 [3600] feet; Stony Clove Notch; Lanesville; Plateau Mountain (all in Catskill Mountains).
Ulster County: Overlook Mountain; Summit [Mountain].
Delaware County: Stamford.

NEW HAMPSHIRE
Coos County: Lancaster; Shelburne; 2 miles by road from summit, and Luckerman's Ravine, Mount Washington.
Grafton County: Franconia.

MAINE
Aroostook County: Fort Fairfield
Somerset County: King and Bartlett Lake.
Washington County: Long Lake.
Hancock County: Bar Harbor.
Knox County: Allen's Island, George's Harbor.
Oxford County: Lake Umbagog; Upton.
York County.

MASSACHUSETTS
Berkshire County: Mount Greylock.
Worcester County: Mount Watatic.

Intermediates between *J. h. hyemalis* and *J. h. carolinensis*

PENNSYLVANIA
Erie County: Tamarack Swamp [8½ miles north-northeast of Edinboro]; Edinboro.
Warren County: Tidioute.
McKean County: Bradford; Katrine Swamp; Norwich; and 3 miles west of Norwich.
Potter County: Newfield Junction; Coudersport; Cherry Spring.
Forest County: Tionesta; Sheffield Junction.
Elk County: 1 mile north of Weedville.
Clinton County: Tamarack Swamp [= Tamarack, head of Drury Run].
Clarion County: Clarion Junction; ½ mile west of Clarion.
Jefferson County: Punxsutawney.
Clearfield County: Winterburn; Woodland.
Lycoming County: North Mountain.
Sullivan County: Lopez.
Luzerne County: Harvey's Lake.
Indiana County: Rochester Mills; Pine Flats.
Cambria County: Belsano; Gallitzin; Cresson; Summit; Portage, 4 miles up Trout River; Dunlo.
Blair County: Allegrippus; Altoona.
Westmorland County: Conemaugh Furnace; Laughlintown.
Fayette County: Sugar Loaf Mountain [= Sugarloaf Knob].
Somerset County: Crumb; Keystone Junction.

MARYLAND
Garrett County: Finzel; Bittinger.

WEST VIRGINIA
Tucker County: Davis.

Junco hyemalis carolinensis

WEST VIRGINIA

Greenbrier County: Cold Knob; Job's Knob.

VIRGINIA

Page County: Stony Man.
Rockbridge County: Davis.
Bedford County: White Top, Peaks of Otter.
Giles County: Mountain Lake.
Tazewell County: Tazewell.
Grayson County: Mount Rogers; Trout Dale.

KENTUCKY

Harlan County: Big Black Mountain.

TENNESSEE

Carter County: top Roan Mountain.

NORTH CAROLINA

Avery County: Cranberry.
Mitchell County: 5500–6300 feet and summit of Roan Mountain.
Yancey County: Mount Mitchell, 6000–6300 feet.
Buncombe County: Black Mountain; Craggy Mountain, 6300 feet.
Macon County: Highlands.

GEORGIA

Towns County: Brasstown Bald, 4500 feet.
Gilmer County: Rich Mountain, 4000 feet.

Intermediates between *J. h. cismontanus* and *J. h. hyemalis*

YUKON

Lake Marsh.

ALBERTA

Edmonton region; 25 miles northwest of Edmonton; Lac La Nonne; 12 miles west of St. Ann's; Edmonton; Camrose; Buck Lake; near Red Deer; Red Deer River at Alta; Red Deer River, 7 miles below Nevis.

Junco hyemalis cismontanus

(Asterisk denotes known presence of *J. o. montanus* or hybrids in same region.)

YUKON

Carcross; Caribou Crossing.

BRITISH COLUMBIA

Skeena District: Bennett City; Atlin; Monarch Mountain, 4500 feet, Atlin; Telegraph Creek; 4–12 miles north of Telegraph Creek; second south fork, 50 miles east Telegraph Creek; Glenora, Stikine River; Doch-da-on Creek, Stikine River; Kispiox Valley,* 23 miles north Hazelton; Nine-Mile Mountain,* 4000 feet, northeast Hazelton.

Cariboo District: Tupper Creek;* Moose Pass;* Yellowhead Pass.*

ALBERTA

Peace River District: Henry House;* Jasper House, and 5 miles south of Jasper House; Smoky River, Moose Branch; Jasper Park* [= east side of divide]; Brule Lake;* Prairie Creek; 140 miles west Edmonton.

Hybrids between *J. h. cismontanus* (or *J. h. hyemalis*) and *J. o. montanus*

ALASKA

Mountains near Eagle.

BRITISH COLUMBIA

Kispiox Valley, 23 miles north of Hazelton; Nine-Mile Mountain, 4000 feet, northeast of Hazelton.

Cariboo District: Tupper Creek; Cottonwood; Indianpoint Lake; 12 miles north of Clearwater.

West Kootenay District: Rossland; Creston.

East Kootenay District: Field; Cranbrook.

ALBERTA

Peace River District: Jasper Park [= east side of divide]; Brule Lake; Brazeau Lake.

Athabasca District: Fort McMurray (essentially *montanus;* breeding?).

Junco aikeni

SOUTH DAKOTA

Lawrence County: Spearfish, 4600 feet; Deadwood (October 6).

Custer County: Custer.

WYOMING

Crook County: Sundance.

NEBRASKA

Sioux County: Monroe Canyon [Hat Creek] (August 18; molting wing).

MONTANA

Powder River County: 4 miles west of Fort Howe Ranger Station, 4000 feet (also 3 *aikeni* × *mearnsi*).

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Transmitted by author May 19, 1938; but corrections and some additions made up to November 15, 1940.—A. H. M.